

CHARLES DARWIN AND THE ORIGIN OF SPECIES

ADDRESSES, ETC., IN AMERICA AND ENGLAND
IN THE YEAR OF THE TWO ANNIVERSARIES

BY

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TO
ALFRED RUSSEL WALLACE

WHO GAVE TO HIS BOOK ON NATURAL SELECTION
THE TITLE 'DARWINISM', THIS COLLECTION
OF ADDRESSES ON DARWIN AND THE
'ORIGIN' IS AFFECTIONATELY
DEDICATED

REFERENCE

PREFACE

DURING the fourteen months preceding the date on which this volume is issued I have devoted all available time to work connected with the three inspiring anniversaries of July 1, 1908, Feb. 12, 1909, and Nov. 24, 1909. With all diffidence I have chosen the date which closes this period of work, as the day of publication. It may help in some small degree to keep in remembrance the birthday of a mighty epoch in the history of thought.

The first Section of this book attempts to give a brief account of the history which led up to and followed the publication of the theory of Natural Selection and the *Origin of Species*. Darwin's sure scientific insight, and his views on evolution by mutation, briefly treated in this Section, receive further consideration in Appendices A and B. The confusion of thought threatened by the unintentional but most unfortunate misrepresentation of de Vries's term, 'fluctuating variability,' is pointed out in a footnote and further considered in Appendix D. I have given at the end of this Appendix a very brief account of certain phases of thought, during the past

half century, on the variations forming the material out of which the steps of evolutionary progress have been supposed to be built.

The influence of Darwin's personality upon the intellectual revolution of the past fifty years is considered in the second Section. The widespread misunderstanding of the changes which Darwin describes in his own mind, and the consequent injustice to scientific men generally, and especially to Darwin himself, not only form the subject of argument and protest in this Section, but also occupy nearly all the brief third Section, part of the seventh, and the whole of Appendix C.

The unfortunate misinterpretations referred to above require, for their complete and final refutation, the collection from Darwin's correspondence of a large number of passages bearing upon health. These, placed together, may convey to the hasty reader an entirely wrong impression of Darwin's heroic spirit, and I therefore trust that the words on p. 216 will be remembered whenever such passages may be read.

In the fourth Section the relationship of Darwin to the two ancient English Universities, and especially to his own University of Cambridge, is very briefly considered.

The fifth Section is concerned with one of the first and still perhaps the most striking of the

interpretations that have sprung from the theory of Natural Selection. The subject, 'the Value of Colour in the Struggle for Life,' is treated historically. Darwin's own hypotheses and discoveries in this line, and his keen interest in the hypotheses and discoveries of others are especially considered here and also in part of the seventh Section.

The sixth Section deals with Mimicry, the most arresting of all the uses which colour may subserve in the struggle for existence. It is maintained that this complicated subject is best approached by the study of North American examples, and attention is directed to the number of inspiring problems which await a thorough and systematic attack by American naturalists.

Darwin's hitherto unpublished letters to Mr. Roland Trimen, F.R.S., form the subject of the seventh Section. An interesting account of Mr. Trimen's first meeting with the illustrious naturalist fifty years ago is also included. In addition to the eighteen letters in Section VII, four written by Darwin to other correspondents are published in this volume—one in Section I, two in Section V, and one in Section VI. I desire to thank my friends for generously lending me these twenty-two deeply interesting letters, and Mr. Francis Darwin for kindly permitting their publication.

The occasions on which the addresses here printed were delivered are described in an introductory note at the beginning of each Section. Three out of the seven Sections of this volume, viz. I, IV, and V, have already appeared; four are now published for the first time.

I have especial reasons for being grateful to my American friends for permission to reprint the address contained in the first Section. The Publication Committee of the American Association for the Advancement of Science did me the honour of choosing the title of my address as the title of the complete work—*Fifty Years of Darwinism*,—containing the eleven centennial addresses, in honour of Charles Darwin, delivered on Jan. 1, 1909. The publishers who owned the copyright were very doubtful about the success of the work—unnecessarily as it happened, for I understand that a second edition is already being prepared. In spite of considerations which seemed at the time to be weighty, both Committee and Publishers at once granted me the most free and cordial permission to reprint the address in the present work.

The Syndics of the Cambridge University Press generously allowed the publication, on Nov. 24, of Section V, which had appeared as Essay XV of *Darwin and Modern Science* only eight months

earlier, the Preface being dated March 20, 1909. I also desire to acknowledge the kind permission to publish Section IV from *Darwin Celebration, Cambridge, June, 1909. Speeches delivered at the Banquet held on June 23rd*, printed for private circulation by Sir George Darwin and Mr. Francis Darwin.

In these later years the multitudes seem, for the moment at least, to recognize a prophet in every reed shaken with the wind. It would be interesting to know the number of forgotten works, of works soon to be forgotten, of works dead before they were born, which have been proclaimed as 'the most important contribution to biological thought since the appearance of the *Origin of Species*'. I would that the multitudes were not mere followers of the fleeting scientific fashions of a day, but that they were right in their intuitions: I would that Newtons and Darwins might arise in every generation. I cannot admit that the inability to see them on every side is merely the natural consequence of a cynical and pessimistic spirit. I am fully aware of the intellectual rigidity that is so prone to develop with the passing years; but to know the danger is in some measure to be armed against it. I have steadily endeavoured to keep my mind elastic and flexible; and, in my own special

line of work, have again and again abandoned the most dearly loved hypothesis when a new interpretation was seen to be more consistent with an ever-growing store of facts. And I submit that it is even more difficult to keep an open mind in the pursuit of a special line of research than in the consideration of the broadest and most far-reaching problems which confront the human intellect.

Although the splendidly thorough work of the present day must rightly compel the warmest admiration, there are valid reasons why we should direct a searching and critical gaze upon the proclamation of each enthusiastic specialist that the foundations of organic evolution are wholly surrounded by the boundaries of his own field of inquiry. Organic evolution, to be understood, must be studied not in the light of one special line of work, but of all. This was the great secret of Darwin's unique power in dealing with it. He could see the subject from all sides. And an ample measure of Darwin's strength was possessed by his great comrades of half a century ago. How we long for a little of the sure insight and comprehensive vision of Asa Gray as we read the address of his distinguished living representative, Professor J. M. Coulter, who considers that an adaptive response to environment is destructive of Natural Selection, and finds it hard to imagine

how Darwinism can account for the valuable mechanical functions of lifeless structures.' And even more arresting is the contrast between Darwin's outlook on the world of life and that of the eminent Dutch botanist who raised fresh strains, or perhaps sorted over again old mixtures of Evening Primroses, and straightway said to his friends: 'Go to, let us build us an exalted theory of evolution based on the conception of an inborn transforming force violently discharged at regular intervals by every species of times past, present, and to come.' And the historic fate of the too-ambitious builders of Babel is already evident; for, when Professor de Vries, Professor Bateson, and Mr. R. C. Punnett begin to talk of variability in its commonest form, their language is confounded, 'that they may not understand one another's speech.'² And when we remember that the two last-named authorities are the recognized English exponents of the views of the first-named, it will be realized that the confusion which has resulted from the misunderstanding of the words 'acquired character' and the word 'Mimicry' is as nothing to the confusion worse confounded which is even now upon us. The misunderstanding of de Vries by his exponents does however help us to solve one mystery,—the

¹ *Fifty Years of Darwinism*, New York (1909), 61-5. See also the *Quarterly Review* (July, 1909), 7

² See 49, and Appendix D, 258.

extraordinary and,—as many naturalists think,—the unwarrantable exaggeration of the importance of the Dutch botanist's contributions to evolution. *Omne ignotum pro magnifico*. If de Vries had indeed proved, as his exponents assert, that the 'individual differences' in which Darwin saw the steps of evolutionary progress—the 'individual differences' whose behaviour in heredity is the life-work of Francis Galton—that these are in fact non-transmissible to offspring, then surely the greatness of him who demonstrated such a discovery to the world might be justly measured by the depth of the error into which his predecessors had fallen. I need hardly say that de Vries makes no such claim, but, on the contrary, shows us again and again that hereditary transmission to offspring is essential to his conception of 'fluctuating variability'.

For de Vries's laborious and original investigations every one must feel the warmest admiration. He and his friend Professor Hubrecht have always been most anxious to emphasize their conclusion that the *Mutationstheorie* is Darwinian, and they are equally anxious to disown and discredit any attempts to use it as a weapon against Darwin. They have even fallen into the error of maintaining that Darwin anticipated de Vries in holding the main conclusion of the *Mutationstheorie*—the origin of species by the selection of large

single variations.¹ It is with great reluctance that I have protested against the unduly important position which, as I believe, is assigned to de Vries's work and conclusions in the history of evolution

The Darwinian of the present day holds an intermediate position between the followers of Buffon and Lamarck, and the Mutationists, with whom the Mendelians are somewhat unnecessarily allied. The disciple of the two first-named naturalists, in these days calling himself an oecologist, maintains that organisms are the product of their environment: the Mutationist holds that organisms are subject to inborn transformation, and that environment selects the fittest from among a crowd of finished products. The Darwinian believes that the finished product or species is gradually built up by the environmental selection of minute increments, holding that, among inborn variations of all degrees of magnitude, the small and not the large become the steps by which evolution proceeds. He attempts to avoid, as Darwin did, on the one hand the error of ascribing the species-forming forces wholly to a creative environment, and, on the other, the perhaps more dangerous error of ascribing them wholly to creative internal tendencies.

¹ Both professors of course admit that Darwin also believed in an evolution founded on the selection of 'individual differences'.

The failure of the earlier attacks on the *Origin* has been referred to in many pages of this book ; but my chief object throughout has been to speak of Darwinism and of Darwin himself. Hence Mendelism, entirely unknown to the illustrious naturalist, is on this occasion barely mentioned.¹ The conception of evolution by mutation, on the other hand, is shown to have been from the first entirely familiar to Darwin, and entirely rejected by him. In the *Quarterly Review*² for July, 1909, I have ‘endeavoured to set forth—necessarily with brevity—the chief results of those modern investigations which, after fifty years, are now believed to be charged with menace for the Darwin-Wallace hypothesis’; and I will conclude by quoting the final words of the article: ‘The inspiration of these investigations has attracted a numerous band of enthusiastic and devoted labourers, who have achieved and are achieving results of the highest interest and importance. No one of these, it is here maintained, can be reasonably held to make good the claims of the modern opponent of natural selection and evolution as conceived by Darwin. The only fundamental changes in the doctrine given to us

¹ See however the close of Appendix D. Attention is directed in Section VI to certain North American butterflies which appear to afford a peculiarly favourable opportunity of testing the working of Mendel’s law under natural conditions.

² ‘The Centenary of Darwin Darwin and his Modern Critics,’ 1-38.

in 1858 and 1859 are those brought about by the researches and the thoughts of Weismann ; and these have given to the great theory which will ever be associated with the names of the two illustrious English naturalists a position far higher than that ever assigned to it by Darwin himself.'

EDWARD B. POULTON.

OXFORD,

Nov. 24, 1909.

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I

FIFTY YEARS OF DARWINISM

One of the centennial addresses in honour of Charles Darwin, read before the American Association for the Advancement of Science, Baltimore, Friday, January 1, 1909. Revised and extended.

ON this historic occasion it is of special interest to reflect for a few moments on the part played by the New World in the origin and growth of the great intellectual force which dominates the past half-century. The central doctrine of evolution, quite apart from any explanation of it, was first forced upon Darwin's mind by his South American observations during the voyage of the *Beagle*; and we may be sure that his experience in this same country, teeming with innumerable and varied forms of life, confirmed and deepened his convictions as to the importance of adaptation and thus prepared the way for Natural Selection. Wallace, too, at first travelled in South America, and only later in the parts of the Old World tropics which stand next to South America in richness.

Asa Gray in the New World represents Sir Joseph Hooker in the Old, as regards the help given to Darwin before the appearance of

a letter¹ written to Huxley, probably in 1859, and published since the appearance of Professor Osborn's book, indicates that Charles Darwin suspected the French naturalist of borrowing from his grandfather:—

‘The history of error is quite unimportant, but it is curious to observe how exactly and accurately my grandfather (in *Zoonomia*, vol. i., p. 504, 1794) gives Lamarck's theory. I will quote one sentence. Speaking of birds' beaks, he says: “All which seem to have been gradually produced during many generations by the perpetual endeavour of the creatures to supply the want of food, and to have been delivered to their posterity with constant improvement of them for the purposes required.” Lamarck published *Hist. Zoolog.* in 1809. The *Zoonomia* was translated into many languages’

A careful comparison of the French translation of the *Zoonomia* with Lamarck's *Philosophie Zoologique* and with a preliminary statement of his views published in 1802, would probably decide this interesting question.

THE INFLUENCE OF LYELL UPON CHARLES DARWIN

The limits of space compel me to pass by the youth of Charles Darwin, with the influence of school, Edinburgh and Cambridge, including his intimacy with Henslow—a friendship leading to the voyage in the *Beagle*. We must also pass by his earliest convictions on evolution, the

‘acquired’ in the sense of ‘acquired characters’; ‘changement acquis’ is the form employed many years later by Lamarck.

¹ *More Letters of Charles Darwin* Edited by Francis Darwin and A. C. Seward, London, 1903, i. 125. Hereafter quoted as *More Letters*.

first note-book begun in 1837, the reading of Malthus and discovery of Natural Selection in October, 1838, the imperfect sketch of 1842, the completed sketch of 1844.

It is necessary, however, to pause for a brief consideration of the influence of Sir Charles Lyell. Although the writings of the illustrious geologist have always been looked upon as among the chief of the forces brought to bear upon the mind of Darwin, evidence derived from the later volumes of correspondence justifies the belief that the effect was even greater and more significant than has been supposed.

Huxley has maintained with great force that the way was paved for Darwin by Lyell's *Principles of Geology* far more thoroughly than by any other work.

' . . . consistent uniformitarianism postulates evolution as much in the organic as in the inorganic world. The origin of a new species by other than natural agencies would be a vastly greater "catastrophe" than any of those which Lyell successfully eliminated from sober geological speculation.'¹

When the first volume of the *Principles* appeared in 1830, Darwin was advised by Henslow to obtain and study it, 'but on no account to accept the views therein advocated.' Darwin took the volume with him on the voyage, and a study of the very first place at which the *Beagle* touched,

¹ *Life and Letters of Charles Darwin*, edited by Francis Darwin, London, 1887, II. 190 Hereafter quoted as *Life and Letters*.

St. Jago, one of the Cape de Verde Islands, showed him the infinite superiority of Lyell's teachings.¹

He wrote in 1876 : 'The science of Geology is enormously indebted to Lyell—more so, as I believe, than to any other man who ever lived.'² An even more remarkable tribute to his old teacher is paid by Darwin in the following words written to L. Horner, August 29, 1844 :—

'I have lately been reading with care A. d'Orbigny's work on South America, and I cannot say how forcibly impressed I am with the infinite superiority of the Lyellian school of Geology over the continental. I always feel as if my books came half out of Lyell's brain, and that I never acknowledge this sufficiently ; nor do I know how I can without saying so in so many words—for I have always thought that the great merit of the *Principles* was that it altered the whole tone of one's mind, and therefore that, when seeing a thing never seen by Lyell, one yet saw it partially through his eyes—it would have been in some respects better if I had done this less'

This letter was written not two months after the date which marks the completion of the finished sketch of 1844. On July 5, Darwin wrote the letter to his wife begging her, in the event of his death, to arrange for the publication of the account he had just prepared. At this psychological moment in his career he wrote of the influence received from Lyell, and we are naturally led to observe how essentially Lyellian

¹ *Life and Letters*, i 62, 72, 73.

² l. c, 72

³ *More Letters*, ii 117.

are the three lines of argument—two based on geographical distribution, one on the relation between the living and the dead—which first led Darwin toward a belief in evolution. The thoughts which shook the world arose in a mind whose whole tone had been altered by Lyell's teachings. Inasmuch as the founder of modern geology received his first inspiration from Buckland, Oxford may claim some share in moulding the mind of Darwin.¹

It is deeply interesting to set beside the evidence of Darwin's debt to Lyell the words in which Lyell gives us some conception of what Darwin's friendship—even in its early days—meant for him. Not long after Darwin's marriage (Jan. 29, 1839), when he and his wife were contemplating leaving London for the country, Lyell wrote:—

'I cannot tell you how often since your long illness I have missed the friendly intercourse which we had so frequently before, and on which I built more than ever after your marriage. It will not happen easily that twice in one's life, even in the large world of London, a congenial soul so occupied with precisely the same pursuits and with an independence enabling him to pursue them will fall so nearly in my way, and to have had it snatched from me with the prospect of your residence somewhat far off is a privation I feel to be a very great one.'²

¹ See also pp. 86, 87.

² July ?, 1841?. *More Letters*, i 31 Darwin left London for Down on Sept. 14, 1842.

‘ COMING EVENTS CAST THEIR SHADOWS
BEFORE ’

The characteristic feature in which Natural Selection differs from every other attempt to solve the problem of evolution is the account taken of the struggle for existence, and the rôle assigned to it. Professor Osborn¹ refers to the keen appreciation of this struggle in Tennyson's noble poem, *In Memoriam*, the dedication of which is dated 1849, ten years before the *Origin*. The poet is disquieted by :—

‘ Nature red in tooth and claw
With ravine, ’

and by

‘ . . . finding that of fifty seeds
She often brings but one to bear.’

It is interesting to note that the obvious understatement of this last passage is corrected in the author's notes published by his son a few years ago. In these we find ‘for fifty, read myriad’. The poignant sense of the waste of individual lives is brought into close relation in the poem with the destruction of the type or species :—

‘ So careful of the type she seems,
So careless of the single life ; ’

‘ “ So careful of the type ? ” but no,
From scarp'd cliff and quarried stone
She cries “ A thousand types are gone :
I care for nothing, all shall go ” .’

¹ *From the Greeks to Darwin*, New York, 1894, 141.

In this association between the struggle for existence waged by individuals and the extinction and succession of species we seem to approach the central idea of Darwin and Wallace. A few years before Tennyson's death I asked Dr. Grove, of Newport, in the Isle of Wight, if he would point out the parallelism, so far as it existed, to his illustrious patient, hoping that some light might be thrown on the source of the inspiration. Nor was I disappointed. 'Stay,' said the aged poet when Dr. Grove had spoken, '*In Memoriam* was published long before the *Origin of Species*.' 'Oh! then you are the man,' replied the doctor. 'Yes, I am the man.' There was silence for a time; then Tennyson said: 'I don't want you to go away with a wrong impression. The fact is that long before Darwin's work appeared these ideas were known and talked about.' From this deeply interesting conversation I think it is probable that, perhaps through mutual friends, some echo of Darwin's researches and thoughts had reached the great author of *In Memoriam*.¹

The light which has been recently thrown² upon Philip Gosse's remarkable book, *Omphalos*, indicates that its appearance in 1858 was connected with the thoughts that were to arouse

¹ In a valuable letter on Darwin and Tennyson in *The Spectator* for Aug. 7, 1909 (pp. 197, 198), the Rev F. St. John Thackeray points out that the poet was from his youth deeply interested in evolution, and that in 1837 he studied Lyell's *Principles*. It is shown above, however, that the appreciation of the struggle for existence is an essentially Darwinian idea.

² In *Father and Son*, London, 1907.

the world in the following year. The author of *Omphalos* was a keen and enthusiastic naturalist held fast in the grip of the narrowest of religious creeds. We learn with great interest that he and others were by Lyell's advice prepared beforehand for the central thoughts of the *Origin*. To the new teaching all the naturalist side of his nature responded, but from it the religious side recoiled. Religion conquered in the strife, but the naturalist found comfort in the perfectly logical conclusion that : —

‘any breach in the circular course of nature could be conceived only on the supposition that the object created bore false witness to past processes, which had never taken place.’¹

Thus the divergence between the literal interpretation of Scripture and the conclusions of both geologist and evolutionist were for this remarkable man reconciled by the conviction :

‘that there had been no gradual modification of the surface of the earth, or slow development of organic forms, but that when the catastrophie act of creation took place, the world presented, instantly, the structural appearance of a planet on which life had long existed.’²

Philip Gosse could not but believe that the thoughts which had brought so much comfort to himself would prove a blessing to others also. He offered *Omphalos* ‘with a glowing gesture, to atheists and Christians alike. . . . But, alas ! atheists and Christians alike looked at it and laughed, and threw it away’.³ Charles Kingsley

¹ l. c., 120, 121

² l. c., 120

³ l. c., 122

expressed the objection felt by the Christian when he wrote that he could not 'believe that God had written on the rocks one enormous and superfluous lie'.¹

About twenty years ago I was present when precisely the same conclusion was advanced by a high dignitary of the English Church. He argued that even if the history of the Universe were carried back to a single element such as hydrogen, the human mind would remain unsatisfied and would inquire whence the hydrogen came, and that any and every underlying form of matter must leave the inexorable question 'whence?' still unanswered. Therefore if in the end the question must be given up, we may as well, he argued, admit the mystery of creation in the later stages as in the earlier. Thus he arrived at the belief in a world formed instantaneously, ready-made and complete, with its fossils, marks of denudation, and evidences of evolution — a going concern. Aubrey Moore, the clergyman who more than any other man was responsible for breaking down the antagonism towards evolution then widely felt in the English Church, replied very much as Kingsley had done, that he was unwilling to believe that the Creator had deliberately cheated the intellectual powers. He had

¹ Ibid. It is possible that Darwin was referring to *Omphalos* when he wrote, Sept. 2, 1859, to Lyell, 'our posterity will marvel as much about the current belief as we do about fossil shells having been thought to have been created as we now see them.' *Life and Letters*, ii. 165

made. I may add that, inasmuch as science consists in the attempt to carry down causation as far as possible, it is above all the scientific side of the human intellect that is outraged—no weaker term can be used—by this more modern development of the argument of *Omphalos*.

THE PUBLICATION OF THE DARWIN-WALLACE ESSAY

In May, 1856, Darwin, urged by Lyell, began to prepare for publication. He had determined to present his conclusions in a volume, for he was unwilling to place any responsibility for his opinions on the Council of a Scientific Society. On this point, he was, as he told Sir Joseph Hooker, in the only fit state for asking advice, namely, with his mind firmly made up: 'then . . . *good* advice was very comfortable, and it was easy to reject *bad* advice.'¹ The work was continued steadily until June 18, 1858, when Wallace's letter and essay arrived from Ternate. As a result of the anniversary held in London on July 1, 1908, new light has been thrown upon the circumstances under which the joint essay was published fifty years before.

In consequence of the death of the eminent botanist, Robert Brown, Vice-President and Ex-President of the Linnean Society, the last meeting of the summer session, called for June 17, was adjourned. The bye-laws required that the

¹ *Life and Letters*, ii. 70. See also 68, 69, 71.

vacancy on the Council should be filled up within three months, and a special meeting was called for July 1 for this purpose. Darwin received Wallace's essay on June 18, too late for the summer meetings of the Society, but in good time for Lyell and Hooker to present it to the special meeting. Hence, as Sir Joseph Hooker said on July 1, 1908, the death of Robert Brown caused the theory of Natural Selection to be 'given to the world at least four months earlier than would otherwise have been the case'. Sir Joseph Hooker also informed us that from June 18, up to the evening of July 1, when he met Sir Charles Lyell at the Society, all the intercourse with Darwin and with each other was conducted by letter, and that no fourth person was admitted into their confidence. The joint essay was read by the Secretary of the Society. Darwin was not present, but both Lyell and Hooker 'said a few words to emphasise the importance of the subject'.¹ Among those who were present were Oliver, Fitton, Carpenter, Henfrey, Burchell, and Bentham,² who was elected

¹ *Darwin Wallace Celebration of the Linnean Society of London* (1908), 14, 15.

² July 1, 1858, was an important date in the life of the great botanist George Bentham. He had himself prepared for that very meeting a long paper illustrating what he believed to be the fixity of species. 'Most fortunately my paper had to give way to Mr. Darwin's, and when once that was read, I felt bound to defer mine for reconsideration; I began to entertain doubts on the subject, and on the appearance of the "Origin of Species", I was forced, however reluctantly, to give up my long-cherished convictions, the results of much labour and study, and I cancelled all that part of my paper which urged original fixity.' *Life and Letters*, ii. 294. See also the *Quarterly Review* (July, 1909), 6.

on the Council and nominated as Vice-President in place of Robert Brown.

I cannot resist the temptation to reprint from the memorial volume issued by the Linnean Society of London some passages in the address which A. R. Wallace felt constrained to deliver on July 1, 1908, protesting against the too great credit which he believed had been assigned to himself. After describing Darwin's discovery of Natural Selection and the twenty years devoted to confirmation and patient research, Wallace continued :—

‘How different from this long study and preparation—this philosophic caution—this determination not to make known his fruitful conception till he could back it up by overwhelming proofs—was my own conduct. The idea came to me, as it had come to Darwin, in a sudden flash of insight. it was thought out in a few hours—was written down with such a sketch of its various applications and developments as occurred to me at the moment,—then copied on thin letter-paper and sent off to Darwin—all within one week. I was then (as often since) the “young man in a hurry”: *he*, the painstaking and patient student, seeking ever the full demonstration of the truth that he had discovered, rather than to achieve immediate personal fame.

‘Such being the actual facts of the case, I should have had no cause for complaint if the respective shares of Darwin and myself in regard to the elucidation of nature's method of organic development had been thenceforth estimated as being, roughly, proportional to the time we had each bestowed upon it when it was thus first given to the world—that is to say, as 20 years is to one week. For, he had already made it his own. If the persuasion of his friends had prevailed with him, and he had published

his theory, after 10 years'—15 years'—or even 18 years' elaboration of it—I should have had no part in it whatever, and *he* would have been at once recognised, and should be ever recognised, as the sole and undisputed discoverer and patient investigator of the great law of "Natural Selection" in all its far-reaching consequences.

'It was really a singular piece of good luck that gave me any share whatever in the discovery. . . it was only Darwin's extreme desire to perfect his work that allowed me to come in, as a very bad second, in the truly Olympian race in which all philosophical biologists, from Buffon and Erasmus Darwin to Richard Owen and Robert Chambers, were more or less actively engaged.'¹

ECHOES OF THE STORM

It is impossible to do more than refer briefly to the storm of opposition with which the *Origin* was at first received. The reviewer in the *Athenaeum* for Nov. 19, 1859, left the author 'to the mercies of the Divinity Hall, the College, the Lecture Room, and the Museum'.² Dr. Whewell for some years refused to allow a copy of the *Origin* to be placed in the library of Trinity College, Cambridge.³ My predecessor, Professor J. O. Westwood, proposed to the last Oxford University Commission the permanent endowment of a lecturer to combat the errors of Darwinism. 'Lyell had difficulty in preventing [Sir William] Dawson reviewing the *Origin* on hearsay, without having looked at it. No spirit of fairness can be expected from so biassed

¹ *Darwin-Wallace Celebration of the Linnean Society of London* (1908), 6, 7.

² *Life and Letters*, II 228 n.

³ *Ibid.*, 261 n.

a judge.’¹ And even when naturalists began to be shaken by the force of Darwin’s reasoning, they were often afraid to own it. Thus Darwin wrote to H. Fawcett, on Sept. 18, 1861 :—

‘Many are so fearful of speaking out. A German naturalist came here the other day; and he tells me that there are many in Germany on our side, but that all seem fearful of speaking out, and waiting for some one to speak, and then many will follow. The naturalists seem as timid as young ladies should be, about their scientific reputation.’²

Among the commonest criticisms in the early days, and one that Darwin felt acutely,³ was the assertion that he had deserted the true method of scientific investigation. One of the best examples of this is to be found in the letter of Darwin’s old teacher in geology, Adam Sedgwick :—

‘You have *deserted*—after a start in that tram-road of all solid physical truth—the true method of induction, and started us in machinery as wild, I think, as Bishop Wilkins’s locomotive that was to sail with us to the moon.’⁴

This ill-aimed criticism was soon set to rest by Henry Fawcett’s article in *Macmillan’s Magazine*

¹ From a letter written by Darwin to Hooker, Nov. 4, 1862. *More Letters*, i 468.

² *More Letters*, i 196.

³ See Darwin’s letter to Henslow, May 8, 1860. *More Letters*, i, 149, 150.

⁴ *Life and Letters*, ii 248. Sedgwick’s letter is dated Dec. 24, 1859, but the editors of *More Letters* (i. 150 n.) express the opinion that it must have been written in November at latest. See also the *Quarterly Review* for July, 1860. Sedgwick’s review in the *Spectator*, Mar. 24, 1860, contains the following passage: ‘... I cannot conclude without expressing my detestation of the theory, because of its unflinching materialism;—because it has deserted the inductive track, the only track that leads to physical truth;—because it utterly repudiates final causes, and thereby indicates a demoralised understanding on the part of its advocates.’ Quoted in *Life and Letters*, ii 298.

in 1860, and by a paper read before the British Association by the same author in 1861. Referring to this defence Fawcett wrote to Darwin, July 16, 1861 :—

‘I was particularly anxious to point out that the method of investigation pursued was in every respect philosophically correct. I was spending an evening last week with my friend Mr. John Stuart Mill, and I am sure you will be pleased to hear from such an authority that he considers that your reasoning throughout is in the most exact accordance with the strict principles of logic. He also says the method of investigation you have followed is the only one proper to such a subject.

‘It is easy for an antagonistic reviewer, when he finds it difficult to answer your arguments, to attempt to dispose of the whole matter by uttering some such commonplace as “This is not a Baconian induction”. . . .

‘As far as I am personally concerned, I am sure I ought to be grateful to you, for since my accident nothing has given me so much pleasure as the perusal of your book. Such studies are now a great resource to me.’¹

To this Darwin replied :—

‘You could not possibly have told me anything which would have given me more satisfaction than what you say about Mr. Mill’s opinion. Until your review appeared I began to think that perhaps I did not understand at all how to reason scientifically.’²

In the general truth of his theory Darwin felt an entire confidence born of the long years of pondering over difficulties throughout the whole realm of natural history. And it was the consciousness that a secure and undisturbed belief lay behind the fair and cautious statements of the

¹ *More Letters*, i 189, 190.

² *Ibid.*, 189.

Origin that was so intensely irritating to men whose antagonism was based on religious conviction. Thus in Sedgwick's letter, from which I have already quoted, we read :—

‘Lastly, then, I greatly dislike the concluding chapter—not as a summary, for in that light it appears good—but I dislike it from the tone of triumphant confidence in which you appeal to the rising generation . . . and prophecy of things not yet in the womb of time, nor (if we are to trust the accumulated experience of human sense and the inferences of its logic) ever likely to be found anywhere but in the fertile womb of man's imagination.’¹

THE MATURITY OF THE ORIGIN CONTRASTED WITH THE CRUDITY OF RIVAL INTERPRETATIONS

It is remarkable to contrast the maturity, the balance, the judgement, with which Darwin put forward his views, with the rash and haphazard objections and rival suggestions advanced by critics. It is doubtful whether so striking a contrast is to be found in the history of science—on the one side, twenty years of thought and investigation pursued by the greatest of naturalists; on the other, off-hand impressions upon a most complex problem hastily studied and usually very imperfectly understood. It is not to be wondered at that Darwin found the early criticisms so entirely worthless. The following extract from an interesting letter to John Scott,

¹ *Life and Letters*, II. 250.

written on Dec. 3, 1862?, shows how well aware he was of difficulties unnoticed by critics :—

‘ You speak of difficulties on Natural Selection : there are indeed plenty ; if ever you have spare time (which is not likely, as I am sure you must be a hard worker) I should be very glad to hear difficulties from one who has observed so much as you have. The majority of criticisms on the *Origin* are, in my opinion, not worth the paper they are printed on.’¹

From the very first the most extraordinarily crude and ill-considered suggestions were put forward by those who were unable to recognize the value of the theory of Natural Selection. A good example is to be found in Andrew Murray’s principle of sexual selection based on contrast :—

‘ It is trite to a proverb, that tall men marry little women . . . a man of genius marries a fool . . . and we are told that this is the result of the charm of contrast, or of qualities admired in others because we do not possess them. I do not so explain it. I imagine it is the effort of nature to preserve the typical medium of the race.’²

Even in these later years the wildest imaginings may be put forward in all seriousness as the interpretation of the world of living organisms. Thus in Beccari’s interesting work on Borneo,³ the author compares the infancy and growth of the organic world with the development and education of an individual. In youth the individual learns easily, being unimpeded by the

¹ *More Letters*, ii, 311.

² *Life and Letters*, ii, 261 n. The original paper is to be found in the *Proc. R. Soc. Edin.*, 1860.

³ *Wanderings in the Great Forests of Borneo*, 209-16, English translation, London, 1904.

force of habits, while 'with age heredity acts more strongly, instincts prevail, and adaptation to new conditions of existence and to new ideas become more difficult ; in a word, it is much less easy to combat hereditary tendencies'. Similarly, in the state of maturity now reached by the organic world, Beccari believes that the power of adaptation is wellnigh non-existent. Heredity, through long accumulation in the course of endless generations, has become so powerful that species are now stereotyped and cannot undergo advantageous changes. For the same reason, he considers, acquired characters cannot now be transmitted to offspring. Beccari imagines that everything was different in early ages, when, as he supposes, life was young and heredity weak. In this assumed 'Plasmatic Epoch' the environment acted strongly upon organisms, evoking the responsive changes which have now been rendered fixed and immovable by heredity.

Even the hypothesis proposed as a substitute for Natural Selection by so distinguished a botanist as Carl Nageli turns out to be most unsatisfactory the moment it is examined. The idea of evolution under the compulsion of an internal force residing in the idioplasm is in essence but little removed from special creation. On the subject of Nageli's criticisms Darwin wrote, Aug. 10, 1869, to Lord Farrer :—

'It is to me delightful to see what appears a mere morphological character found to be of use. It pleases me the more

as Carl Nägeli has lately been pitching into me on this head. Hooker, with whom I discussed the subject, maintained that uses would be found for lots more structures, and cheered me by throwing my own orchids into my teeth.' ¹

DARWIN'S GREATEST FRIENDS IN THE TIME OF STRESS

It is interesting to put side by side passages from two letters² written by Darwin to Hooker, one in 1845 at the beginning of their friendship, the other thirty-six years later, a few months before Darwin's death. The first shows the instant growth of their friendship: 'Farewell! What a good thing is community of tastes! I feel as if I had known you for fifty years. Adios.'

The second letter expresses at the end of Darwin's life the same feelings which find utterance ever and again throughout the long years of his friendship (see pp. 66, 67).

'Your letter has cheered me, and the world does not look a quarter so black this morning as it did when I wrote before. Your friendly words are worth their weight in gold.'

It was to Hooker that Darwin first confided, Jan. 11, 1844, his belief in evolution, but did not at the time, even to him, give any account of natural selection:—

'At last gleams of light have come, and I am almost convinced (quite contrary to the opinion I started with) that

¹ *More Letters*, II 380.

² *Ibid.*, I. 39. The passages here quoted are placed side by side by the editors of this work.

species are not (it is like confessing a murder) immutable. . . . I think I have found out (here's presumption!) the simple way by which species become exquisitely adapted to various ends. You will now groan, and think to yourself, "on what a man have I been wasting my time and writing to." I should, five years ago, have thought so . . .'¹

Elaborate investigations of all kinds during the long years which led up to the central work of Darwin's life were discussed in detail with the greatest of his friends, and it was an inestimable advantage that the ideas of the *Origin* were thus searchingly tried beforehand by so critical and, in the best sense, sceptical a mind as Hooker's—'you terrible worrier of poor theorists!'² as Darwin called him. Again in 1868:—

'I have got your photograph over my chimney-piece, and like it much; but you look down so sharp on me that I shall never be bold enough to wriggle myself out of any contradiction'³

The friendship with Asa Gray began with a meeting at Kew some years before the publication of *Natural Selection*. Darwin soon began to ask for help in the work which was ultimately to appear as the *Origin*. The following letter to Hooker, June 10, 1855, shows what he thought of the great American botanist:—

'I have written him a very long letter, telling him some of

¹ *Life and Letters*, ii. 23, 24. See also on p. 32 the letter, dated Oct. 12, [1845], in which Darwin confided his belief 'that species are mutable' to the Rev. L. Jenyns (Blomefield). The passage from a letter dated Feb 14, 1845, to the same correspondent, quoted on p 42 n 1, suggests that the communication of Oct. 12 was written in 1844 and not 1845.

² Feb. 28, [1858]. *More Letters*, i 105

³ *More Letters*, ii 376, 377.

the points about which I should feel curious. But on my life it is sublimely ridiculous, my making suggestions to such a man.'¹

The friendship ripened very quickly, so that on July 20, 1856, Darwin gave Asa Gray an account of his views on evolution,² and on Sept. 5 of the following year, a tolerably full description of Natural Selection.³ From this last letter Darwin chose the extracts which formed part of his section of the joint essay published July 1, 1858.

Asa Gray's opinion on first reading the *Origin* was expressed not to Darwin but to Hooker in a letter written Jan. 5, 1860 :—

'It is done in a *masterly manner*. It might well have taken twenty years to produce it. It is crammed full of most interesting matter—thoroughly digested—well expressed—close, cogent, and taken as a system it makes out a better case than I had supposed possible. . . .'

After referring to Agassiz's unfavourable opinion of the book he continues: 'Tell Darwin all this. I will write to him when I get a chance. As I have promised, he and you shall have fair-play here. . . .'⁴ A little later, when on Jan. 23 he wrote to Darwin himself, Asa Gray concluded: 'I am free to say that I never learnt so much from one book as I have from yours. There remain a thousand things I long to say about it.'⁵

¹ *More Letters*, 1. 418. Asa Gray's generous reply appears on p. 421.

² *Life and Letters*, 11. 78

³ *Ibid*, 120-5.

⁴ *Ibid.*, 268.

⁵ *Ibid*, 272

It is impossible to do justice on the present occasion to the numerous letters in which Darwin expressed his gratitude for the splendid manner in which Asa Gray kept his word and fought 'like a hero in defence'.¹ At a time when few naturalists were able to understand the drift of Darwin's argument, the acute and penetrating mind of Asa Gray had in a moment mastered every detail. Thus Darwin wrote on July 22, 1860, concerning the article in the *Proceedings of the American Academy* for April 10 :—

' . . . I cannot resist expressing my sincere admiration for your most clear powers of reasoning. As Hooker lately said in a note to me, you are more than *any one* else the thorough master of the subject. I declare that you know my book as well as I do myself, and bring to the question new lines of illustration and argument in a manner which excites my astonishment and almost my envy! . . . Every single word seems weighed carefully, and tells like a 32-pound shot.'²

Some weeks later, on Sept. 26, 1860, Darwin again expressed the same admiration, and stated that Asa Gray understood him more perfectly than any other friend :—

' . . . you never touch the subject without making it clearer. I look at it as even more extraordinary that you never say a word or use an epithet which does not express fully my meaning. Now Lyell, Hooker, and others, who perfectly understand my book, yet sometimes use expressions to which I demur.'³

¹ *Life and Letters*, II. 310.

² *Ibid.*, 326.

³ *Ibid.*, 344, 345.

Darwin also sent¹ Asa Gray's defence of the *Origin* to Sir Charles Lyell, whom he was extremely anxious to convince of the truth of evolution. Asa Gray's religious convictions prevented the full acceptance of Natural Selection. He was ever inclined to believe in the Providential guidance of the stream of variation. He also apparently differed from Darwin in the extent to which he was inclined to interpret instincts as inherited habits.²

The same close intimacy and mutual help begun in the preparation of the *Origin* was continued in Darwin's later botanical works. Thus Darwin owed his *Climbing Plants* to the study of a paper by Asa Gray, and he dedicated his *Forms of Flowers* to the American botanist 'as a small tribute of respect and affection'. Concerning some of the researches which afterwards appeared in this book, Darwin wrote:—

'I care more for your and Hooker's opinion than for that of all the rest of the world, and for Lyell's on geological points.'

Another great name, that of Huxley, is especially associated in our minds with the defeat of those who would have denied that the subject was a proper one for scientific investigation. In the strenuous and memorable years that followed the appearance of the *Origin*, the mighty warrior stands out as the man to whom

¹ *More Letters*, i. 169.

² *Life and Letters*, iii 170

³ *Ibid.*, 300.

more than to any other we owe the gift of free speech and free opinion in science,—the man so admirably described by Sir Ray Lankester at the Linnean Celebration as ‘the great and beloved teacher, the unequalled orator, the brilliant essayist, the unconquerable champion and literary swordsman—Thomas Henry Huxley’.¹

Comparing the friendships to which Darwin owed so much, Lyell was at first the teacher but finally the pupil,—unwilling and unconvinced at the outset, in the end convinced although still unwilling; Hooker in England and Asa Gray in America were the two intimate friends on whom Darwin chiefly depended for help in writing the *Origin*, and for support to its arguments; Huxley was the great general in the field where religious convictions, expressed or unexpressed, were the foundation of a fierce and bitter antagonism.

THE ATTACKS OF RICHARD OWEN AND ST. GEORGE MIVART

An unnecessary bitterness was imported into the early controversies in England, because of the personality of the scientific leaders in the attacks on the *Origin*. Of these the chief was the great comparative anatomist, Sir Richard Owen. In spite of his leading scientific position, this remarkable man withdrew from contact with his brother zoologists, living in a self-imposed isola-

¹ *Darwin-Wallace Celebration of the Linnean Society of London* (1908), 29. See also pp 66-8 of the present work.

tion which tended towards envy and bitterness. The same unavailing detachment had been carried much further by the great naturalist W. J. Burchell, who, as from a watch-tower, looked upon the world he strove to avoid with an absorbed and jealous interest. Prof. J. M. Baldwin has shown how inevitable and inexorable is the grip of the social environment: the more we attempt to evade it, the more firmly we seem to be held in its grasp.

In the first years of the struggle, Owen's bitter antagonism made itself felt in the part he took as 'crammer' to the Bishop of Oxford, and in his anonymous article in the *Edinburgh Review* for April, 1860. But Owen could not bear to remain apart from the stream of thought when there was no doubt about the way it was flowing, so that in a few years he was maintaining some of the chief conclusions of the *Origin*, although retracting nothing, but rather keeping up a bitter attack upon Darwin. This treatment received from one who was all affability when they met,¹ was naturally resented by Darwin, whose feelings on the subject are expressed in the following passage from a letter to Asa Gray, July 23, 1862.

'By the way, one of my chief enemies (the sole one who has annoyed me), namely Owen, I hear has been lecturing on birds; and admits that all have descended from one, and advances as his own idea that the oceanic wingless birds

¹ 'Mis. Carlyle said that Owen's sweetness always reminded her of sugar of lead.' *Life and Letters of T. H. Huxley*, London, II. 167.

have lost their wings by gradual disuse. He never alludes to me, or only with bitter sneers, and coupled with Buffon and the *Vestiges*.'¹

In the historical sketch added to the later editions of the *Origin*, Owen is the only writer who is severely dealt with. In this introductory section Darwin said that he was unable to decide whether Owen did or did not claim to have originated the theory of Natural Selection.²

If Owen had withdrawn from his former attitude of antagonism, as did Lyell, he would be entitled to the same honourable place in the memory of future generations. As it is, we must regret that he did not keep up the struggle to the

¹ *More Letters*, 1 203.

² *Origin of Species*, 6th Ed., xviii. See also the writer's article in the *Quarterly Review* for July, 1909, 4-6. The following remarkable episode, which I owe to the kindness of my friend Mr. Roland Trimen, F.R.S., is quoted from p. 5.—

'At Down, about the end of the year 1867, when conversing with Mr. Darwin about the already steadily increasing acceptance of the "*Origin*" among thinking naturalists, in contrast to the active hostility it encountered on and long after its first appearance only eight years before, I referred to the heavy artillery brought to bear against it in the "*Quarterly*" and "*Edinburgh*" Reviews, besides the host of other discharges from arms of minor calibre. Mr. Darwin asked me if I knew who wrote the "*Edinburgh*" article, and on my replying that I did not, but that I had heard Owen's name suggested amongst others, he said, "Owen was the man." I ventured to enquire whether he came to this conclusion from other evidence than that afforded by the style, tone, etc., of the article itself, and he answered, "The internal evidence made me almost sure that only Owen could have written it; but when I taxed him with the authorship and he absolutely denied it—then I was quite certain."

'Words of such keen satire came with extraordinary effect from a man so eminently gentle and considerate, and so free from any touch of jealousy or self-assertion as Darwin. They made a deep and lasting impression on me—all the more because they were spoken very quietly and deliberately, and because they were the only words of censure I heard used by the greatest of naturalists.'

end. How completely he abandoned it, and how sharp was the contrast between him and a still surviving warrior of the 'Old Guard', remains as one of my earliest and clearest memories of the scientific world. The stage was the meeting of the British Association at York, in 1881, when Prof. O. C. Marsh described the Berlin skeleton of *Archaeopteryx*. The lizard-like characteristics of the earlier fossil in the British Museum—bought, it was said, at the price of a dowry for a professor's daughter—were far more clearly displayed in the later find. Prof. Marsh told me that he would have given almost any sum to secure this—probably the most valuable and interesting fossil in the world—for the museum at Yale. 'I dare not do it,' was the reply. 'We let the other go, and I really believe they would kill me if I sold this one.' So Prof. Marsh, obliged to study the wonderful ancestral bird in Berlin, came, fresh from his work, to tell us about it at York.

Owen, presiding over the zoological section at which the paper was read, seemed quite enthusiastic over *Archaeopteryx*, and had not a word of criticism for the evolutionary history which it unfolded. He discoursed sweetly upon the teeth, believed to have been discovered in embryonic parrots, and, with his suave manner and venerable appearance, created a very pleasant impression. An entirely different scene was enacted, a day or two later, in the geological section, where Prof.

H. G. Seeley exhibited a restoration of the same fossil. Dr. Wright, the palaeontologist, old and deaf, but staunch as ever, would have none of it. 'Archaeopteryx hasn't got a head. How can it possibly have teeth?' he asked angrily, thinking of the older specimen in the British Museum. But even in this, the remains of the head, detached from the body, had been made out by Sir John Evans in a corner of the block of oolite, while the teeth were found scattered over the surface of the stone. Prof. Newton's emphatic assertion that the bird had teeth left him quite unshaken, and even after Prof. Marsh, called on by the chairman, had drawn their form on the blackboard, and the section was proceeding to other business, Dr. Wright could be heard muttering savagely, 'Archaeopteryx is a very good bird.' And its excellence was in his opinion obviously incompatible with reptilian affinity. Disbelief in evolution was with him a matter of faith and could never have been affected by any amount of evidence.

About twelve years after the appearance of the *Origin*, another opponent, St. George Mivart, produced something of the same bitterness as Owen, and for a similar reason. Thus Darwin wrote to Hooker, Sept. 16, 1871, as follows:—

'You never read such strong letters Mivart wrote to me about respect towards me, begging that I would call on him, etc., etc.; yet in the *Q. Review* [July, 1871] he shows the greatest scorn and animosity towards me, and with un-

common cleverness says all that is most disagreeable. He makes me the most arrogant, odious beast that ever lived. I cannot understand him; I suppose that accursed religious bigotry is at the root of it. Of course he is quite at liberty to scorn and hate me, but why take such trouble to express something more than friendship? It has mortified me a good deal.'¹

On other occasions at a much later date I have myself observed that there was something peculiar about the poise of Mivart's mind, which seemed ever inclined to pass, with abrupt transition, from the extreme of an unnecessary effusiveness to an unnecessarily extreme antagonism.

Mivart's attack, contained in his book, *The Genesis of Species*, was effectively dealt with by Chauncey Wright in the *North American Review* for July, 1871. Darwin was so pleased with this defence that he obtained the author's permission for an English reprint,² and with further additions it was published as a pamphlet by John Murray in 1871. A copy presented by Darwin to the late J. Jenner Weir, and now in the library of the Hope Department of the Oxford University Museum, contains an interesting holograph letter referring to the pamphlet and bearing upon the controversy that followed upon the appearance of Mivart's book. This letter is, by kind permission of Mr. Francis Darwin, now made public:—

¹ *More Letters*, i. 333. See also *Life and Letters*, iii. 146-50.

² The pamphlet was published at Darwin's expense. For his keenly appreciative letters to the author, see *Life and Letters*, iii. 145, 146.

Down,
Beckenham, Kent.
Oct. 11, 1871.

MY DEAR SIR

I am much obliged for your kind note and invitation. I sh^d like exceedingly to accept it, but it is impossible. I have been for some months worse than usual, and can withstand no exertion or excitement of any kind, and in consequence have not been able to see anyone or go anywhere.—As long as I remain quite quiet, I can do some work, and I am now preparing a new and cheap Editⁿ of the Origin in which I shall answer Mr. Mivart's chief objections. Huxley will bring out a splendid review on d^o in the Contemporary R., on November 1st.

I am pleased that you like Ch. Wright's article. It seemed to me very clever for a man who is not a naturalist. He is highly esteemed in the U. States as a Mathematician and sound reasoner.

I wish I could join your party.—

My dear Sir

Yours very sincerely

CH DARWIN.¹

Chauncey Wright speaks of presenting, in his review of Mivart, considerations 'in defence and illustration of the theory of Natural Selection. My special purpose,' he continues, 'has been to contribute to the theory by placing it in its proper relations to philosophical inquiries in general.'²

This able critic in America, and Henry Fawcett in England, represent a class of thinkers who have taken and still take a very important part in upholding the theory of Natural Selection. It

¹ The letter is addressed to J. Jenner Weir, Esq., 6 Haddo Villas, Blackheath, London, S E.

² In a letter to Darwin, June 21, 1871. *Life and Letters*, iii. 143, 144.

is not necessary to be a biologist in order to comprehend the details and the bearings of this theory. At the outset, when naturalists themselves were often hopelessly puzzled, the theory was clearly understood by able thinkers who were not students of biology, or indeed in some cases of any of the sciences. And at the present time such support is of the highest importance when, within the boundaries of the sciences most nearly concerned, the intense and natural desire to try all things is not always accompanied by the steadfast purpose to hold fast that which is good.

LAMARCK'S HYPOTHESIS AND THE HEREDITARY TRANSMISSION OF ACQUIRED CHARACTERS

The greatest change in evolutionary thought, since the publication of the *Origin*, was wrought, after Darwin's death, by the appearance of that wonderful and beautiful theory of heredity which looks on parents as the elder brother and sister of their children. In this theory, itself an outcome of minute and exact observation (see p. 39), Weismann raised the question of the hereditary transmission of acquired characters, the very foundation of Lamarckian and Spencerian evolution. Darwin accepted this transmission, and it was in order to account for 'such facts as the inherited effects of use and disuse, &c.,'¹ that he thought out his marvellous hypothesis of

¹ See the letter to Huxley, July 12 (1865 ?), in *Life and Letters*, iii. 44.

pangeneses. If such effects be not transmitted, pangeneses becomes unnecessary and Weismann's simpler, more convincing, and better supported hypothesis of the continuity of the germ-plasm takes its place. It is impossible on the present occasion to speak in any detail of the controversy which has raged intermittently during the past twenty years on this fascinating subject. I will, however, briefly consider a single example of the error into which, as I believe, Darwin was led by following the Lamarckian theory of hereditary experience. I refer to the interpretation which he suggests for feelings of 'the sublime', applying this term to the effect upon the brain of a vast cathedral, a tropical forest, or a view from a mountain height. Thus, writing to E. Gurney, July 8, 1876, Darwin said on this subject: '... possibly the sense of sublimity excited by a grand cathedral may have some connection with the vague feelings of terror and superstition in our savage ancestors, when they entered a great cavern or gloomy forest.'¹

An interesting account is given by Romanes² of Darwin's own experience of these feelings, relating how he at first thought that they were most excited by the magnificent prospect surveyed from one of the summits of the Cordilleras, but afterwards came down from his bed on purpose to correct this impression, saying that he felt most of the sublime in the forests of Brazil.

¹ *Life and Letters*, iii. 186.

² *Ibid.*, 54, 55. See also i. 64, 65.

We may first observe that the remarkable feelings induced by such experiences are very far from unpleasant, as we should expect them to be on the theory which refers them to the apprehensions and dangers of our primitive ancestors. Thus, on May 18, 1832, when the first impressions of a Brazilian forest were freshest in Darwin's mind, he wrote to Henslow, telling him of an expedition of 150 miles from Rio de Janeiro to the Rio Macao.

'Here I first saw a tropical forest in all its sublime grandeur—nothing but the reality can give any idea how wonderful, how magnificent the scene is. . . . I never experienced such intense delight. I formerly admired Humboldt, I now almost adore him; he alone gives any notion of the feelings which are raised in the mind on first entering the Tropics.'¹

Furthermore, how are we to account on any such hypothesis for the similarity of the feelings excited by the forest, where enemies might lurk unseen, and the mountain peak, the very spot which offers the best facility for seeing them? It is also difficult to understand why the terrors of primitive man should be specially associated with caves or with the most magnificent forests on the face of the earth.² There is no valid reason for believing that any less danger lurked amid trees of ordinary size or lay in wait for him by the riverside, in the jungle, or the rock-strewn

¹ *Life and Letters*, i. 236, 237.

² There is grave doubt whether the New World was inhabited by man until long after the Palaeolithic Age.

waste. In the midst of life he was in death in every solitary place that could afford cover to an enemy ; on the mountain-top probably least of all.

The feelings inspired by the interior of a cathedral are especially instructive in seeking the explanation of the psychological effect. We may be sure that the result is here produced by the unaccustomed scale of the aesthetic impression. A cathedral the size of an ordinary church would not produce it. However intensely we may admire, the sense of the sublime is not excited or but feebly excited by the exterior of a cathedral, nor does it accompany the profound intellectual interest aroused by the sight of the Pyramids. The thrill of the sublime, in the sense in which the term is here used, is, I do not doubt, the result of surprise and wonder raised to their highest power—a psychological shock at the reception of an aesthetic visual experience on an unwonted scale—vast, as if belonging to a larger world in which the insignificance of man is forced upon him. It is not excited by the Pyramids, which are in form but symmetrical hills of stone, nor does the exterior of any building afford an experience sufficiently remote to produce the feeling in any high degree.

W. J. Burchell, in one of his letters¹ to Sir William Hooker, points out that the feelings of awe and wonder aroused in a Brazilian forest

¹ Preserved in the Library at Kew, but, I believe, as yet unpublished.

are not to be expected in those to whom the sight is familiar. As regards the depth and nature of the effects produced by the experiences here referred to, it would be very interesting to compare the savage with the civilized man, the uneducated with the educated mind. That the results are intimately bound up with the psychological differences between individuals—in part inherent, in part due to training and experience—is well illustrated in a story told by the late Charles Dudley Warner, who took two English friends to see for the first time the Grand Canyon of the Colorado. When they reached the point where the whole prospect—boundless beyond imagination—is revealed in a moment of time, one of his friends burst into tears, while the other relieved his feelings by unbridled blasphemy.

The remarkable psychological effects of a grandeur far transcending and far removed from ordinary experience may be compared to the thrill¹ so often felt on hearing majestic music—a thrill we do not seek to explain as a faint, far-off reminiscence of dread inspired by the savage war-cry. I do not doubt that an explanation of the sublime based on the terrors of our primitive ancestors is an example of the mistaken interpretations into which even Darwin was led by following the hypothesis of Lamarck.

¹ Darwin spoke of his backbone shivering during the anthem in King's College chapel. *Life and Letters*, i 49, see also 170.

FRANCIS DARWIN ON THE TRANSMISSION OF
ACQUIRED CHARACTERS

One of the most recent attempts to defend the Lamarckian doctrine of the hereditary transmission of acquired characters is contained in the important Presidential Address of Mr. Francis Darwin to the British Association at Dublin (1908). In this interesting memoir the author expresses the belief that such transmission is implied by the persistence for unnumbered generations of the successive developmental stages through which the individual advances towards maturity. Following Hering and Richard Semon, he is disposed to explain the hereditary transmission of these stages by a process analogous to memory. It is interesting to observe that this very analogy had been brought before Charles Darwin, but failed to satisfy him. He wrote to G. J. Romanes, May 29, 1876 :—

‘I send by this post an essay by Haeckel attacking Pan. and substituting a molecular hypothesis. If I understand his views rightly, he would say that with a bird which strengthened its wings by use, the formative protoplasm of the strengthened parts became changed, and its molecular vibrations consequently changed, and that these vibrations are transmitted throughout the whole frame of the bird, and affect the sexual elements in such a manner that the wings of the offspring are developed in a like strengthened manner. . . . He lays much stress on inheritance being a form of unconscious memory, but how far this is part of his molecular vibration, I do not understand. His views make nothing clearer to me ; but this may be my fault.’¹

¹ *More Letters*, 1 364. See also the following sentence in a letter

Should it hereafter be proved that acquired characters are inherited, I cannot but think that the interpretation will be on the lines of Charles Darwin's hypothesis of Pangenesis. But the probability that any such result will be established, already shown to be extremely small, has become even more remote in the light of the recent investigations conducted by Mendelians and Mutationists.

For the transmission of all inherent qualities, including the successive stages of individual development, Weismann's hypothesis of the continuity of the germ-plasm supplies a sufficient mechanism. I remember, more than twenty years ago, asking this distinguished discoverer how it was that the hypothesis arose in his mind. He replied that when he was working upon the germ-cells of Hydrozoa he came to realize that he was dealing with material which—early and late in the history of the individual—was most carefully preserved, as though it were of the most essential importance for the species. If

on Pangenesis, written June 3, 1868, to Fritz Muller —‘It often appears to me almost certain that the characters of the parents are “photographed” on the child, only by means of material atoms derived from each cell in both parents, and developed in the child.’ —*More Letters*, ii. 82: also quoted in *Life and Letters*, iii. 84. The following passage in a letter to Sir Joseph Hooker, Feb. 28, 1868, is also of great interest. —‘When you or Huxley say that a single cell of a plant, or the stump of an amputated limb, has the “potentiality” of reproducing the whole—or “diffuses an influence”, these words give me no positive idea;—but, when it is said that the cells of a plant, or stump, include atoms derived from every other cell of the whole organism and capable of development, I gain a distinct idea’—*Life and Letters*, iii. 81.

the efficient cause of the stages of individual development (ontogeny) resides in the fertilized ovum—as we cannot doubt—then Weismann's hypothesis satisfactorily accounts for their hereditary transmission. For the portion of the ovum set aside to form the germ-cells from which the next generation will arise is reserved with all its powers, and includes the potentiality of these stages no less than the other inherent characteristics of the individual.

It is, I think, unfortunate to seek for analogies—and vague analogies they must always be—between heredity and memory. However much we have still to learn about it, memory is, on its physiological side, a definite property of certain higher cerebral tissues,—a property which has clearly been of the utmost advantage in the struggle for life, and bears the stamp of adaptation. Compare, for instance, the difficulty in remembering a name with the facility in recognizing a face. Adaptation would appear to be even more clearly displayed in the unconscious registration in memory and the instant recognition of another individual as seen from behind or when partially concealed. Such memory is quite independent of the artistic power. Without any intelligent appreciation of what is peculiar to another individual, his characteristic features are stored up unconsciously, so that when seen again he is instantly recognized.

One other consideration brought forward by

Mr. Francis Darwin may be briefly discussed. It is well known that plants have the power of adjusting themselves to their individual environment, and that such adjustment may beneficially take the place of a rigid specialization. The fixed condition of plants renders this power especially necessary for them, and the hereditary transmission of the results of its exercise especially dangerous. Where the seed falls, there must the plant grow. The parent was limited to one out of many possible environments; the offspring may grow in any of them, and for one that would hit off the precise conditions of the parent and would benefit by inheriting the parental response, numbers would have to live in different surroundings and might be injured by the hereditary bias.

Mr. Francis Darwin calls attention to the leaves of the beech, which in the interior shaded parts of the tree possess a structure different from that exhibited on the outer parts more freely exposed to light. The structure of the shaded leaves resembles that apparently stereotyped in trees always adapted to shade, and Mr. Francis Darwin is inclined to regard the permanent condition as a final result of the hereditary transmission of the same response through a large number of generations.

The development of shade foliage in the beech is, I presume, a manifestation of a power widely spread among animals and probably among plants also—a power of producing a definite individual

adaptation in response to a definite stimulus. To stereotype the result would be to convert a benefit to the individual into an injury to the species. The beech in a very shady place would presumably develop the maximum of the shade foliage. How disadvantageous would the hereditary bias be to its offspring that happened to grow in more exposed situations. But, it is argued, in plants subject to a permanent condition we do meet with a permanent structure, just as if repetition had at length produced a hereditary result. The answer to this argument seems to me to be complete. When conditions are uniform and no power of individual adaptation is required, Natural Selection, without attaining the power, would produce the permanent and hereditary result in the usual way. If, however, a species, already possessing the power, ultimately came to live permanently in one set of conditions and thus ceased to need it, the power itself, no longer sustained by selection, would sooner or later be lost.

DARWIN'S VIEWS ON EVOLUTION BY 'MUTATION'

It is interesting to note that the word 'Mutation' appears at one time to have suggested itself to Darwin¹ in order to express the evolution or

¹This seems clear from the following passage in a letter written Feb. 14 [1845], to Rev. L. Blomefield (Jenyns) 'Thanks for your hint about terms of "mutation", etc., I had some suspicions that it was not quite correct, and yet I do not yet see

descent with modification of species, by no means implying change by large and sudden steps as in the usual modern acceptation of the term. Indeed, the words 'mutable', 'mutability', and their opposites, have never been employed with the special significance now attached to 'mutation'. Every one believes in the mutability of species, but opinions differ as to whether they change by mutation.

It is a mistake to suppose that Darwin did not long and carefully consider large variations, or 'mutations', as supplying the material for evolution. Writing to Asa Gray as early as August 11, 1860, he said of great and sudden variation :—

'I have, of course, no objection to this, indeed it would be a great aid, but I did not allude to the subject, for, after much labour, I could find nothing which satisfied me of the probability of such occurrences. There seems to me in almost every case too much, too complex, and too beautiful adaptation, in every structure to believe in its sudden production.'¹

In the twenty years between 1860 and 1880 we find that Darwin was continually brought back to this subject by his correspondents, and by reviews and criticisms of his works. Scattered over this period we find numbers of letters in which he expressed his disbelief in an evolution founded

my way to arrive at any better terms. It will be years before I publish, so that I shall have plenty of time to think of better words. Development would perhaps do, only it is applied to the changes of an individual during its growth.'—*More Letters*, i. 50. See also p. 22 n. 1.

¹ *Life and Letters*, ii. 333.

on 'sudden jumps' or 'monstrosities', as well as on 'large', 'extreme', and 'great and sudden variations' (see Appendix B, p. 254). Out of many examples I select one more because of its peculiar interest.

The Duke of Argyll, in his address to the Royal Society of Edinburgh, Dec. 5, 1864, used the following words:—'Strictly speaking, therefore, Mr. Darwin's theory is not a theory of the Origin of Species at all, but only a theory on the causes which lead to the relative success and failure of such new forms as may be born into the world.'¹ In a letter to Lyell, Jan. 22, 1865, Darwin wrote concerning this argument:—

'I demur . . . to the Duke's expression of "new births". That may be a very good theory, but it is not mine, unless indeed he calls a bird born with a beak $\frac{1}{100}$ th of an inch longer than usual "a new birth"; but this is not the sense in which the term would usually be understood. The more I work, the more I feel convinced that it is by the accumulation of such extremely slight variations that new species arise.'²

We therefore find that when the Duke criticized Darwin's theory of Natural Selection as though it had been founded on mutation, the interpretation was repudiated by Darwin himself.

I desire again to state most emphatically that, during the whole course of his researches and reflections upon evolution, Darwin was thoroughly

¹ *Scotsman*, Dec 6, 1864.

² *Life and Letters*, III. 33. See also *Quarterly Review*, July, 1909, 25, 26, also 10-12

aware of the widespread large variations upon which the mutationist relies. He had the material before him, he formed his judgement upon it, and on this memorable day it seems specially appropriate to show how extraordinarily sure his scientific instincts were wont to be. This will be made clear by a few examples of the solutions which Darwin found for problems which at the time had either not been attempted at all or had been very differently interpreted.

Darwin's explanation of coral islands and atolls, at first generally accepted, was afterwards called in question. Finally, the conclusive test of a deep boring entirely confirmed the original theory. Perhaps the most remarkable case is that of the permanence of ocean basins and continental areas, a view which Darwin maintained single-handed in Europe, although supported by Dana in America, against Lyell, Forbes, Wallace, Hooker and all others who had written on the subject. Darwin considered it mere waste of time to speculate about the origin of life; we might as well, he said, speculate about the origin of matter. Nothing hitherto discovered has shaken this opinion, which is expressed almost in Darwin's words in Prof. Arrhenius' recent work.¹ In the fascinating subject of geographical distribution we now know that Darwin anticipated Edward Forbes in explaining the alpine arctic forms as relics of the glacial period (see

¹ *Worlds in the making*. English transl., London (1908), 218.

p. 123, *n.* 2), while he interpreted the poverty of the Greenland flora and the reappearance of north temperate species in the southern part of South America as results of the same cause. Almost as soon as the facts were before him in Wollaston's memoirs, Darwin had interpreted the number of wingless beetles in oceanic islands as due to the special dangers of flight. He anticipated H. W. Bates' hypothesis of Mimicry, but drove it from his mind because he did not feel confident about the geographical coincidence of model and mimic (see pp. 123, 124). Long before the *Origin* appeared, Darwin had thought over and rejected the idea that the same species could have more than a single origin, or could arise independently in two different countries—a hypothesis very popular in later years, but, I believe, now entirely abandoned (see Appendix A, p. 247).

I should wish to advance one further consideration before concluding this section of my address. Certain writers on mutation seem to hold the view that Natural Selection alone prevents large variations from often holding the field and leading on to great and rapid changes of species. Such a view is not supported by the history of species which inhabit situations comparatively sheltered from the struggle, such as fresh water, caves, certain islands, or the depths of the ocean. Organisms in these places tend to preserve their ancestral structure more persis-

tently than in the crowded areas where Natural Selection holds more potent sway.

The grounds for this conclusion, stated by Darwin half a century ago, should be seriously considered by those who are inclined to follow de Vries in his rash speculations on the periodic mutation of species. The following statements are to be found in Darwin's letters to Lyell:—

‘A monad, if no deviation in its structure profitable to it under its *excessively simple* conditions of life occurred, might remain unaltered from long before the Silurian Age to the present day.’¹

‘With respect to *Lepulosiren*, Ganoid fishes, perhaps *Ornithorhynchus*, I suspect, as stated in the *Origin*, that they have been preserved, from inhabiting fresh-water and isolated parts of the world, in which there has been less competition and less rapid progress in Natural Selection, owing to the fewness of individuals which can inhabit small areas; and where there are few individuals variation at most must be slower.’²

‘I quite agree with you on the strange and inexplicable fact of *Ornithorhynchus* having been preserved, and Australian *Trigonia*, or the Silurian *Lingula*. I always repeat to myself that we hardly know why any one single species is rare or common in the best-known countries. I have got a set of notes somewhere on the inhabitants of fresh water; and it is singular how many of these are ancient, or intermediate forms; which I think is explained by the competition having been less severe, and the rate of change of organic forms having been slower in small confined areas, such as all the fresh waters make compared with sea or land.’³

¹ Oct. 11, 1859. *Life and Letters*, ii 210.

² Feb. 18, 1860. *More Letters*, i. 143. See *Origin of Species*, ed. vi, 83, 112.

³ Sept. 12, 1860. *Life and Letters*, ii 340. See also *Quarterly Review*, July, 1909, 21, 22.

EVOLUTION CONTINUOUS OR DISCONTINUOUS

Darwin fully recognized the limits which may be set to the results achieved by the artificial selection in one direction of individual variations. Thus he wrote, Aug. 7, 1869, to Sir Joseph Hooker :—

‘ I am not at all surprised that Hallett has found some varieties of wheat could not be improved in certain desirable qualities as quickly as at first. All experience shows this with animals; but it would, I think, be rash to assume, judging from actual experience, that a little more improvement could not be got in the course of a century, and theoretically very improbable that after a few thousands [of years] rest there would not be a start in the same line of variation.’¹

The conception of evolution hindered or for a time arrested for want of the appropriate variations is far from new. The hypothesis of organic selection was framed by Baldwin, Lloyd Morgan, and Osborn to meet this very difficulty, as expressed in the following paragraph quoted from the present writer’s address to the American Association for the Advancement of Science at the Detroit meeting, Oct. 15, 1897 :—

‘ The contention here urged is that natural selection works upon the highest organisms in such a way that they have become modifiable, and that this power of purely individual adaptability in fact acts as the nurse by whose help the species . . . can live through times in which the needed inherent variations are not forthcoming.’²

¹ *More Letters*, i. 314.

² *Development and Evolution*, J. M. Baldwin, New York (1902), 350.

It has already been shown that Darwin entirely recognized the limits which individual variations, or, as they are called by de Vries, 'fluctuations,'¹ may set to the progress achieved by artificial selection, and that he admitted the necessity of waiting for a fresh 'start in the same line'. In this respect he agreed with modern writers on mutation; but differed from them in believing that the fresh start would ultimately be made. He also differed, as has been already abundantly shown, in the magnitude assigned to the variations forming the steps of the onward march of evolution. His observation and study of nature led him to the conviction that large variations, although abundant, were rarely selected, but that evolution proceeded gradually and by small

¹ It is to be feared that confusion will result from Dr. A. E. Shipley's treatment of this subject in his address to the Zoological Section of the British Association at Winnipeg as reported in the *Times* of Aug. 28, 1909. The account of Dr Shipley's address—by now probably widely read—contains the following statement—'Mutations were variations arising in the germ-cells and due to causes of which we were wholly ignorant, fluctuations were variations arising in the body or "soma" owing to the action of external conditions. The former were undoubtedly inherited, the latter very probably not.' The term 'Fluctuation' or 'Fluctuating Variability' has been applied by de Vries to what Darwin called 'individual variability',—'determining the differences which are always to be seen between parents and their children, or between the children themselves' (*Species and Varieties*, H de Vries, 1906, 190). To speak of these differences as 'very probably not' inherited, is to follow neither Darwin, nor Weismann, nor de Vries, but simply to cause gratuitous confusion by questioning an accepted conclusion based upon universal experience. The reported statement as to the nature of fluctuations would, if it were correct, prove that the hereditary transmission of acquired characters takes place on the vastest imaginable scale. But, although no one disputes that fluctuations are hereditary, very few indeed will agree that they are due 'to the action of external conditions', or in other words 'acquired characters'. See Appendix D, p. 258.

steps,—that it was ‘continuous’, not ‘discontinuous’.

In his Presidential Address¹ to the British Association at Cape Town in 1905, Sir George Darwin argued from analogy against the ‘continuous transformation of species’. It is important to observe that the word ‘continuous’ here expresses uniformity in the rate of specific change, and does not refer, as in the present address, to the minuteness of the steps by which the change is effected. The argument itself, which is of great interest, is as follows :—

‘In the world of life the naturalist describes those forms which persist as species ; similarly the physicist speaks of stable configurations or modes of motion of matter ; and the politician speaks of States. The idea at the base of all these conceptions is that of stability, or the power of resisting disintegration. In other words, the degree of persistence or permanence of a species, of a configuration of matter, or of a State depends on the perfection of its adaptation to its surrounding conditions’

After maintaining that the stability of states rises and declines, culminating when it reaches zero in revolution or extinction, and that the physicist witnesses results analogous with those studied by the politician and the historian, the author continues : —

¹ *Report Brit. Assoc* (1905), 8. In this address as originally delivered and printed in *Fifty Years of Darwinism* I fell into the error of believing that Sir George Darwin was advocating evolution by large steps. I was misled by the consideration that the word ‘continuous’ as used in the present address is a subject of controversy among biologists, whereas a ‘continuous transformation’ in Sir George’s sense would not, as I believe, be supported by any naturalist.

‘ These considerations lead me to express a doubt whether the biologists have been correct in looking for continuous transformation of species. Judging by analogy we should rather expect to find slight continuous changes occurring during a long period of time, followed by a somewhat sudden transformation into a new species, or by rapid extinction.’

In order to clear up any doubts about the sense in which the word ‘continuous’ is here employed, the following footnote is appended to Sir George Darwin’s address :—

‘ If we may illustrate this graphically, I suggest that the process of transformation may be represented by long lines of gentle slope, followed by shorter lines of steeper slope. The alternative is a continuous uniform slope of change. If the former view is correct, it would explain why it should not be easy to detect specific change in actual operation. Some of my critics have erroneously thought that I advocate specific change *per saltum*.’

Biologists are doubtless prepared to agree with the author’s conclusions. Indeed, there is no reason for the belief that they have ever looked for a continuous and uniform rate of specific change,—so clear has been the evidence afforded by the persistence of ancestral forms in certain areas as compared with their modification or extinction in others (see pp. 46, 47).

THE FIFTIETH ANNIVERSARY OF THE ORIGIN OF SPECIES—A RETROSPECT

That the *Origin of Species*, of which Darwin said ‘ It is no doubt the chief work of my life ’,¹ should

¹ These words are used in the autobiography (1876). *Life and Letters*, i. 86. See also the following passage in the letter written to Hooker in July, 1844, the month in which Darwin finished the

have been bitterly attacked and misrepresented in the early years of the last half-century is quite intelligible; but it is difficult to understand the position of a recent writer who maintains that the book exercised a malignant influence upon the interesting and important study of species and varieties by means of hybridism. As regards these researches its appearance, we are told, 'was the signal for a general halt';¹ upon them Natural Selection 'descended like a numbing spell';² and, if we are still unsatisfied with his fertility in metaphor, the author offers a further choice between the forty years in the wilderness³ and the leading into captivity.⁴

Francis Galton, in his reply as a recipient of the Darwin-Wallace Medal on July 1, 1908, recalled the effect of the Linnean Society Essay and the *Origin*. The dominant feeling, he said, was one of freedom.⁵ The liberty of which Galton spoke was freely offered to every student of hybridism. No longer brought up against the blank wall of special creation, he could fearlessly follow his researches into all their bearings upon the evolution of species. And this had been clearly

second and full account of his views (see pp. 6, 87): 'I hate argument from results, but on my views of descent, really Natural History becomes a sublimely grand result-giving subject (now you may quiz me for so foolish an escape of mouth). - *Life and Letters*, II 30

¹ *Rep Brit Assoc* (1904), 575

² 1 c., p. 576.

³ *Mendel's Principles of Heredity*, W. Bateson (1902), 104.

⁴ 1 c., p. 208

⁵ *Darwin-Wallace Celebration of the Linnean Society of London* (1908), 26.

foreseen by Darwin when, in 1837, he opened his first notebook and set forth the grand programme which the acceptance of evolution would unfold. He there said of his theory that 'it would lead to study of . . . heredity', that 'it would lead to closest examination of hybridity and generation'. In the *Origin* itself the admirable researches of Kolreuter and Gartner on these very subjects received the utmost attention, and were brought before the world far more prominently than they have ever been either before or since. Furthermore, the only naturalist who can be described as a pupil of Darwin's was strongly advised by him to repeat some of Gartner's experiments.¹ It is simply erroneous to explain the neglect of such researches as a consequence of the appearance of the *Origin* and the study of adaptation. So far from acting as a 'numbing spell' upon any other inquiry, adaptation itself has been nearly as much neglected as hybridism, and for the same reason—the dominant influence upon biological teaching of the illustrious comparative anatomist Huxley, Darwin's great general in the battles that had to be fought, but not a naturalist, far less a student of living nature.

The momentous influence of the *Origin* upon the past half-century, as well as that strange lack

¹ Darwin's letter of Dec 11 1862, to John Scott, contains the following words: 'If you have the means to repeat Gartner's experiments on variations of *Verbascum* or on maize (see the *Origin*), such experiments would be pre-eminently important.' —*More Letters*, i, 221, 222

of the historic sense which alone could render possible the comparisons I have quoted, require for their appreciation the addition of yet another metaphor to the series we have been so freely offered.

The effect of the *Origin* upon the boundless domain of biological thought was as though the sun had at length dispelled the mists that had long enshrouded a vast primaevial continent. It might then perhaps be natural for some primitive chief to complain of the strong new light that was flooding his neighbours' lands no less than his own, thinking in error not inexcusable at the dawning of the intelligence of mankind, that their loss must be his gain.

And now in my concluding words I have done with controversy.

Fifty years have passed away, and we may be led to forget their deepest lesson, may be tempted to think lightly of the follies and the narrowness, as they appear to us, of the times that are gone. This in itself would be a narrow view.

The distance from which we look back on the conflict is a help in the endeavour to realize its meaning. Huxley's Address on *The Coming of Age of the Origin* was a paean of triumph. Tyndall, his friend, further removed from the struggle by the nature of his life-work, realized its pathos when he spoke in his Belfast Address of the pain of the illustrious American naturalist who was forced to recognize the success of the teachings he

could not accept, the naturalist who dictated in the last year of his life the unalterable conviction that these teachings were false.

I name no names, but I think of leaders of organic evolution in this Continent and in Europe, — sons of great men to whom the new thoughts brought deepest grief, men who struggled tenaciously and indomitably against them. And full many a household unknown to fame was the scene of the same poignant contrast, was torn by the same dramatic conflict.

We have passed through one of the world's mighty bloodless revolutions; and now, standing on the further side, we survey the scene and are compelled to recognize pathos as the ruling feature.

The sublime teachings which so profoundly transformed mankind were given by Him who came not to bring peace on earth but a sword. And so it is in all the ages with every high creative thought which cuts deep into 'the general heart of human kind'. It must bring when it comes division and pain, setting the hearts of the fathers against the children and the children against the fathers.

The world upon which the thoughts of Darwin were launched was very different from the world to which were given the teachings of Galileo and the sublime discoveries of Newton. The immediate effect of the first, although leading to the bitter persecution of the great Italian, was re-

stricted to the leaders of the Church ; the influence of the second was confined to the students of science and mathematics, and was slow in penetrating even these. Nor did either of these high achievements of the human intellect seriously affect the religious convictions of mankind. It was far otherwise with the teachings of the *Origin of Species* ; for in all the boundless realm of philosophy and science no thought has brought with it so much of pain, or in the end has led to so full a measure of the joy which comes of intellectual effort and activity, as that doctrine of Organic Evolution which will ever be associated, first and foremost, with the name of Charles Robert Darwin.

II

THE PERSONALITY OF CHARLES DARWIN

Written from the notes of a speech delivered at the Darwin Banquet of the American Association for the Advancement of Science, Baltimore, Jan. 1, 1909

It is of special interest, on the evening of this New Year's Day so happily devoted to the memory of Charles Darwin, to think of the man himself, and trace the influence of his personal qualities in helping to achieve the vast intellectual transformation of the past half-century.

Professor H. H. Turner has shown how nearly the mighty genius of Newton was lost to the world (see pp. 85, 86), and in the case of Darwin the margin of safety appears to have been even narrower. In the first place it was necessary that he should be freed from the continuous labour of income-making and from all those strains which are at times inevitable even in the easiest of professional careers. Darwin always recognized his dependence upon this indispensable condition, and remembered the debt of gratitude which he owed to the ability and generosity of his father. 'You have no idea during how short

a time daily I am able to work. If I had any regular duties, like you and Hooker, I should do absolutely nothing in science,'¹ he wrote to Huxley. But financial independence was not the only nor indeed the most essential condition under which Darwin's life-work became possible. Francis Darwin has told us, in touching and beautiful words, of the loving care with which his father's delicate health was safeguarded and sustained.

'It is, I repeat, a principal feature of his life, that for nearly forty years he never knew one day of the health of ordinary men, and that thus his life was one long struggle against the weariness and strain of sickness. And this cannot be told without speaking of the one condition which enabled him to bear the strain and fight out the struggle to the end.'²

Darwin's life, in the supreme need which can be gathered from these pathetic words, was also brightened by a full measure of the happiness which comes to a father who is devoted to his children. We are told of one of his sons, about four years old, offering him sixpence if he would only leave his work and come and play with them. 'We all knew the sacredness of working

¹ July 20, 1860. *More Letters*, i 158

² *Life and Letters*, i 160. See also the beautiful passage in Darwin's autobiography which expresses his indebtedness to his wife. It was omitted from the *Life and Letters* published during Mrs. Darwin's lifetime, but has now appeared in *More Letters*, i 30. The following sentence from a letter written by Darwin to his brother Erasmus bears upon an opinion that has often been expressed. 'I do not believe it [sea-sickness] was the cause of my subsequent ill-health, which has lost me so many years,' June 30, 1864. *More Letters*, i 247.

time, but that any one should resist sixpence seemed an impossibility.' ¹ His children followed the custom of children in general in making the delightful assumption that their own father's work must be the work of every properly constituted father. Thus, one of Darwin's children is said to have asked in regard to a neighbour 'Then where does he do his barnacles?' ² Similarly, one of my own daughters, at the fascinating age when the letter 'r' is apt to be an insoluble mystery, invented a little romance in which she supposed herself to be the child of a shepherd. A friend, who entered into the spirit of the game, inquired 'Then where's your father?', and received as the most natural answer in the world, 'Oh! he's in his labotwy.'

The interest of regular work was essential for Darwin's health and comfort; while his ill health, by preventing work, raised a barrier against recovery. Thus for the sake of his health everything was subordinated to work; while for the sake of the work his health was watched over with a double care and anxiety.

The inexorable claim of Darwin's precarious health leads naturally to a subject which has been widely misunderstood and treated with much mistaken judgement. In the brief autobiography, written for the members of his family, Darwin states ³ that up to the age of thirty or

¹ *Life and Letters*, i. 136.

² *More Letters*, i. 38

³ *Life and Letters*, i. 100-102, written in 1881. See also 33, 49, and 69, written in 1876

beyond it he took great interest and felt intense delight in poetry and music, and to a less extent in pictures. Thus on the voyage of the *Beagle*, when it was only possible to take a single volume on an expedition, he always chose Milton. Later on in life, he says that his mind underwent a change. He found poetry intolerably dull and could not endure to read a line of it; he also almost lost his taste for pictures and much of his former exquisite pleasure in fine scenery, while music set him thinking too energetically for his comfort. This alteration, described with characteristic candour and simplicity, but with too great modesty, has often been the subject of comment, and Darwin's life has in this respect been pointed to as an example to be avoided. Yet it is easy to understand how the change came on, and why it is only a superficial reading of the facts which can find anything in the illustrious naturalist's career but the finest example for man to look up to and attempt to imitate.

Darwin's weakness of health came on between the return from the voyage in 1836 and the removal from London to Down in 1842, - the very period at which, as he tells us, his aesthetic tastes began to alter.

The ill health seems to have increased rapidly towards the close of this period. Thus he wrote as late as Jan. 20, 1839, of being 'fond of talking' and 'scarcely ever out of spirits',¹ while the letters

¹ *More Letters*, i. 29.

to Fitz-Roy in 1840 and to Lyell in 1841 speak despondently of the prospects of future work and seem to indicate that Darwin felt the weakness even more severely than in the later years of his life.

‘These two conditions—permanent ill-health and a passionate love of scientific work for its own sake—determined thus early in his career, the character of his whole future life. They impelled him to lead a retired life of constant labour, carried on to the utmost limits of his physical power, a life which signally falsified his melancholy prophecy.’¹

It was an inevitable result of this permanent ill health which prevented Darwin in the later years of his life from saying with Huxley, ‘I warmed both hands before the fire of life.’ When his health was at its best Darwin could only work four hours, or at most four and a half hours in the day; when it was worse than usual the period was reduced to an hour or an hour and a half, while for long stretches of time—many months together—he could do no work at all. I have already said that work was necessary for

¹ *Life and Letters*, i. 272 See also iii 91, where Mr. Francis Darwin shows that the necessity for constant labour became even more imperative in later years ‘He could not rest, and he recognized with regret the gradual change in his mind that rendered continuous work more and more necessary to him as he grew older’ The passage refers to the years 1867 and 1868

² The first line of Landor’s beautiful and dignified verse would have been hardly appropriate to Huxley, although singularly so to Darwin —

‘I strove with none, for none was worth my strife.
Nature I loved, and next to Nature, Art
I warmed both hands before the fire of life:
It sinks, and I am ready to depart.’

his health—‘nothing else makes me forget my ever-recurrent uncomfortable sensations,’—and in order to maintain it the most perfect regularity was necessary, the absence of all effort in other directions, all excitement. During his regular hours Darwin worked ‘with a kind of restrained eagerness’, expending his strength up to the furthest possible limit, so that he would suddenly stop in dictating, ‘with the words, “I believe I mustn’t do any more”.’ It is quite clear that, with his health as it was, no other effort was possible to Darwin during that day. Professor Bradley has spoken of the errors of interpretation due to the reading of Shakespeare with a slack imagination;¹ and any literature worth calling literature demands effort on the part of the reader. Effort was the one thing Darwin could not give. The ordering of Darwin’s life was entirely controlled by the two inexorable and interdependent demands of work and health.

‘It was a sure sign that he was not well when he was idle at any times other than his regular resting hours, for, as long as he remained moderately well, there was no break in the regularity of his life. Week-days and Sundays passed by alike, each with their stated intervals of work and rest. It is almost impossible, except for those who watched his daily life, to realise how essential to his well-being was the regular routine that I have sketched and with what pain and difficulty anything beyond it was attempted. Any public appearance, even of the most modest kind, was an

¹ *Shakespeare in Tragedy*, London, 1904, 349

effort to him. In 1871 he went to the little village church for the wedding of his elder daughter, but he could hardly bear the fatigue of being present through the short service.'¹

The holidays and recreations in which men find relief from overwork and gain renewed strength were closed to Darwin. He rarely left his home except when his researches were interrupted by illness, and it was hoped that a change of air or visit to a hydropathic establishment would enable him to resume work on his return home. This alone could bring him comfort, and, although never entirely idle during his enforced absence, for this he was longing all the time. The inevitable conditions under which Darwin could keep up his slender stock of health and strength and continue his work are expressed again and again in his correspondence. A few passages bearing on the subject are quoted below, and others will be found in Appendix C, p. 256; and in the series of nineteen letters to Mr. Roland Trimen on pp. 218-46. References to the limits imposed by health are to be found in nine of these letters, viz. Nos. 4, 5, 6, 7, 8, 14, 17, 18, and 19. Darwin has been wrongly judged by many who have read his autobiography, is still wrongly judged, as will be shown on pp 79, 80, and it is important, by repeated evidence, to show the true cause of the changes which he described in himself.

¹ *Life and Letters*, i 127, 128.

The autobiography (1876) contains these words:—

‘My chief enjoyment and sole employment throughout life has been scientific work; and the excitement from such work makes me for the time forget, or drives quite away, my daily discomfort.’¹

The four following passages are all taken from letters to Sir Joseph Hooker:—

1858. ‘It is an accursed evil to a man to become so absorbed in any subject as I am in mine.’²

1861. ‘. . . I cannot be idle, much as I wish it, and am never comfortable except when at work. The word holiday is written in a dead language for me, and much I grieve at it.’³

1863. The same inability to find enjoyment in a holiday is expressed in the following passage, which also includes a humorous allusion to the ease with which his work was interrupted:—

‘. . . Notwithstanding the very pleasant reason you give for our not enjoying a holiday, namely, that we have no vices, it is a horrid bore. I have been trying for health’s sake to be idle, with no success. What I shall now have to do, will be to erect a tablet in Down Church, “Sacred to the Memory, &c,” and officially die, and then publish books, “by the late Charles Darwin,” for I cannot think what has come over me of late; I always suffered from the excitement of talking but now it has become ludicrous. I talked lately 1½ hours (broken by tea by myself) with my nephew, and I was [ill] half the night. It is a fearful evil for self and family.’⁴

1868. ‘. . . I am a withered leaf for every subject except Science. It sometimes makes me hate Science, though God

¹ *Life and Letters*, i. 79

² Oct. 13. *Life and Letters*, ii. 139

³ Feb. 4. *Ibid.*, ii. 360.

⁴ Jan. 3. *Ibid.*, iii. 5

knows I ought to be thankful for such a perennial interest, which makes me forget for some hours every day my accursed stomach.'¹

Prof. Judd tells of the deep debt to science which Darwin expressed to him on his last visit to Down, and how, having recently become possessed of an increased income,

'he was most anxious to devote what he could spare to the advancement of Geology or Biology. He dwelt in the most touching manner on the fact that he owed so much happiness and fame to the natural-history sciences which had been the solace of what might have been a painful existence . . . I was much impressed by the earnestness, and, indeed, deep emotion, with which he spoke of his indebtedness to Science, and his desire to promote its interests.'²

Final and secure confirmation of the conclusion that Darwin's health and comfort demanded the employment of his whole strength and energy upon scientific work is found in the following touching passage from a letter written, less than a year before his death, to the dearest of his friends:—

'I am rather despondent about myself, and my troubles are of an exactly opposite nature to yours, for idleness is downright misery to me, as I find here, as I cannot forget my discomfort for an hour. I have not the heart or strength at my age to begin any investigation lasting years, which is the only thing which I enjoy; and I have no little jobs which I can do. So I must look forward to Down graveyard as the sweetest place on earth.'³

The dilemma of Darwin's life entirely explains that limitation of interest which has been so often

¹ June 17. *Life and Letters*, ii. 92.

² *Ibid.* in. 352, 353.

³ To Sir Joseph Hooker, June 15, 1881. *More Letters*, ii. 433.

misunderstood, and it is certain that his keenly sympathetic and emotional nature did not in the slightest degree suffer the injury of which he spoke in the autobiography (1881). 'The loss of these tastes [the higher aesthetic tastes] is a loss of happiness, and may possibly be injurious to the intellect, and more probably to the moral character, by enfeebling the emotional side of our nature.'¹ A single example must suffice, but it supplies overwhelming proof. The most dramatic episode in the history of Darwinism was the encounter between Huxley and the Bishop of Oxford on the Saturday (June 30) of the meeting of the British Association at Oxford in 1860.² The scene of the struggle was the northern section of the first floor room stretching along the whole western front of the University Museum, then just finished. Late on Sunday night Hooker wrote to Darwin, giving him 'some account of the awful battles which raged about species at Oxford.' Darwin replied at once, his letter being dated July 2 (Monday):—

'I have been very poorly, with almost continuous bad headache for forty-eight hours, and I was low enough, and thinking what a useless burthen I was to myself and all others, when your letter came, and it has so cheered me ;

¹ *Life and Letters*, i 102.

² A curious and interesting feature of the Saturday meeting was the presence of Darwin's old captain on the *Beagle*, Fitz-Roy, who, in a state of frantic excitement, brandished a bible and kept trying to make impassioned appeals to the authority of 'the Book'. I was told of this incident, as yet I believe unrecorded, by the late Mr. George Griffith; and my friend Dr. A. G. Vernon Harcourt, F.R.S., who was also present, confirms the accuracy of the account.

your kindness and affection brought tears into my eyes. Talk of fame, honour, pleasure, wealth, all are dirt compared with affection; and this is a doctrine with which, I know, from your letter, that you will agree with from the bottom of your heart.’¹

These were the thoughts aroused in Darwin’s mind by tidings of the mighty conflict over ideas which he had brought before the world. The appeal of the new doctrine was to the reason and the reason alone; but the mind of man is something more than an intellectual engine, and we can well understand that here was a man for whom others would fight more fiercely and tenaciously than they would ever have done for themselves.

The touching words written to Hooker must not obscure the fact that Darwin saw and appreciated the whole significance of the fight at Oxford. He well knew its full value, as is clearly proved by other parts of the letter and by those written to Huxley on July 3rd and 20th. In the latter he said :—

‘From all that I hear from several quarters, it seems that Oxford did the subject great good. It is of enormous importance, the showing the world that a few first-rate men are not afraid of expressing their opinion.’²

Twenty years later, only two years before he died, Darwin recalled the great fight in a letter to Huxley on the subject of his lecture ‘On the Coming of Age of the *Origin of Species*,’ given at the Royal Institution, April 9, 1880 :—

‘... I well know how great a part you have played in establishing and spreading the belief in the descent-theory,

¹ *Life and Letters*, ii. 323.

² *Life and Letters*, ii. 324.

ever since that grand review in the *Times* and the battle royal at Oxford up to the present day.’¹

Not less important than Darwin’s attitude towards his friends was his bearing towards opponents,—a bearing admirably described in George Henry Lewes’s review of *Animals and Plants under Domestication* in the *Pall Mall Gazette* :—

‘We must call attention to the rare and noble calmness with which he expounds his own views, undisturbed by the heats of polemical agitation which those views have excited, and persistently refusing to retort on his antagonists by ridicule, by indignation, or by contempt. Considering the amount of vituperation and insinuation which has come from the other side, this forbearance is supremely dignified.’

‘Nowhere has the author a word that could wound the most sensitive self-love of an antagonist ; nowhere does he, in text or note, expose the fallacies and mistakes of brother investigators . . . but while abstaining from impertinent censure, he is lavish in acknowledging the smallest debts he may owe ; and his book will make many men happy.’²

The charming spirit in which Darwin sent a copy of the *Origin* to the great American naturalist, Louis Agassiz, is an excellent example of his bearing towards those whom he knew to be antagonistic :—

‘As the conclusions at which I have arrived on several points differ so widely from yours, I have thought (should you at any time read my volume) that you might think that I had sent it to you out of a spirit of defiance or bravado ; but I assure you that I act under a wholly different frame of

¹ April 11, 1880. *Life and Letters*, iii. 241.

² *Pall Mall Gazette* of Feb. 10, 15, and 17, 1868. The above-quoted passages are well selected by Mr. Francis Darwin. See *Life and Letters*, iii. 76, 77.

mind. I hope that you will at least give me credit, however erroneous you may think my conclusions, for having earnestly endeavoured to arrive at the truth.’¹

To his over-pugnacious friend Haeckel he wrote :—

‘ . . . I think . . . that you will excite anger, and that anger so completely blinds every one, that your arguments would have no chance of influencing those who are already opposed to our views. Moreover, I do not at all like that you, towards whom I feel so much friendship, should unnecessarily make enemies, and there is pain and vexation enough in the world without more being caused.’²

Another and very potent cause of the rapid growth of the new teachings is to be found in Darwin’s attitude towards his readers. It is extraordinarily well described by Francis Darwin in the great *Life and Letters* :—

‘ The tone of . . . the ‘ Origin ’ is charming, and almost pathetic ; it is the tone of a man who, convinced of the truth of his own views, hardly expects to convince others ; it is just the reverse of the style of a fanatic, who wants to force people to believe. The reader is never scorned for any amount of doubt which he may be imagined to feel, and his scepticism is treated with patient respect. A sceptical reader, or perhaps even an unreasonable reader, seems to have been generally present to his thoughts.’³

The mind of man is ever attracted by the flame and the hurricane of war rather than by the appeal of the still small voice of reason. Nevertheless it is by the still small voice that the thoughts of the world are widened and transformed.

¹ Nov 11, 1859. *Life and Letters*, ii. 215.

² May 21, 1867. *Life and Letters*, iii. 69.

³ *Life and Letters*, i. 156.

A good example of Darwin's beautiful and sympathetic treatment of the younger workers who asked for help is to be found in his letter to Prof. E. B. Wilson, quoted on p. 107. John Scott, employed in the Botanical Garden at Edinburgh, writing about his experiments conducted along lines suggested by Darwin's published researches, became, in a measure, a pupil of the illustrious naturalist. For years Darwin devoted much time and thought not only to Scott's work but to giving the encouragement so necessary to a proud, reserved, sensitive man, with qualities very superior to those usually found in the position in which he was placed. 'I should be proud to be the author of the paper,'¹ he wrote, when he had at length persuaded Scott to prepare an account of some of his investigations for the Linnean Society. And referring to its publication he wrote to Hooker:— 'Remember my *urgent* wish to be able to send the poor fellow a word of praise from any one.'² To the same friend he said of Scott's letters, 'these show remarkable talent, astonishing perseverance, much modesty, and what I admire, determined difference from me on many points.'³

A delightful spirit, boyish in its gaiety, is revealed in Darwin's correspondence with his friends, and especially with the greatest of them

¹ Nov. 7, 1863. *More Letters*, ii. 325. The paper was read Feb. 4, 1864, and is published in *Ann. Soc. Journ.*, viii. 1865.

² Jan. 24, 1864. *More Letters*, ii. 326.

³ Apr. 1, 1864. *Ibid.*, ii. 330.

all, Sir Joseph Hooker. The two following passages from letters to Sir Joseph have been selected not only as examples but also because of their intrinsic interest. In the first, Darwin is speaking of the deplorable loss of the ancestral flora of St. Helena.

'You have no faith, but if I knew any one who lived in St. Helena I would supplicate him to send me home a cask or two of earth from a few inches beneath the surface from the upper part of the island, and from any dried-up pond, and thus, as sure as I'm a wriggler, I should receive a multitude of lost plants.'¹

'*Clematis glandulosa* was a valuable present to me. My gardener showed it to me and said, "This is what they call a *Clematis*," evidently disbelieving it. So I put a little twig to the peduncle, and the next day my gardener said, "You see it is a *Clematis*, for it feels." That's the way we make out plants at Down.'²

Although the gardener showed an intelligent understanding of this point in the investigation of climbing plants, he does not appear to have been equally appreciative of other work. Lord Avebury tells the following story:—

'One of his friends once asked Mr. Darwin's gardener about his master's health, and how he had been lately. "Oh!", he said, "my poor master has been very sadly. I often wish he had something to do. He moons about in the garden, and I have seen him stand doing nothing before a flower for ten minutes at a time. If he only had something to do I really believe he would be better."'³

¹ Jan. 15, 1867. *More Letters*, i. 494.

² Apr. 5, 1864. *More Letters*, ii. 330.

³ *The Darwin-Wallace Celebration of the Linnean Society of London* (1908), 57, 58.

From all Darwin's writings there shines forth the most charming sympathy and even affection for the animals and plants which he studied. '... I can hardly believe that *any one* could be so good-natured as to take such trouble and do such a very disagreeable thing as kill babies,' he wrote, referring to a young chicken and nestling pigeon required for his investigations;¹ and in another letter—'I appreciate your kindness even more than before, for I have done the black deed and murdered an angelic little fantail, and a pouter at ten days old.'² 'I love them to that extent I cannot bear to kill and skeletonise them,'³ he wrote of his pigeons a few months later.

The same strong humanity and love of animals is shown in the depth of his feelings on the subject of vivisection. 'It is a subject which makes me sick with horror, so I will not say another word about it, else I shall not sleep to-night.'⁴ At the same time, he had no doubt about the necessity or the wisdom of permitting such experiments, and of course saw clearly that 'the benefits will accrue only indirectly in the search for abstract truth. It is certain,' he continued, 'that physiology can progress only by

¹ To W. D. Fox, Mar. 19 and 27, 1855. *Life and Letters*, ii. 46-8.

² July, 1855. *Ibid*, 50

³ Nov., 1855. *More Letters*, i. 87 n. 1. From the context it appears probable that the letter was written to Sir Joseph Hooker.

⁴ To Sir Ray Lankester, Mar. 22, 1871. *Life and Letters*, iii. 200. See also 199-210.

experiments on living animals. Therefore the proposal to limit research to points of which we can now see the bearings in regard to health, &c., I look at as puerile.'¹ Some years later, only a few weeks before his death, he wrote, referring to Edmund Gurney's articles on vivisection:—

' . . . I agree with almost everything he says, except with some passages which appear to imply that no experiments should be tried unless some immediate good can be predicted, and this is a gigantic mistake contradicted by the whole history of science.'²

We also meet with clear evidence of Darwin's love, almost always humorously expressed, for the children of his brain, his hypotheses. Thus, when studying the development of tendrils, he was able to show a beautiful gradation between these organs and leaves, but was utterly puzzled by the vine, in which they are known to be modified branches. He discussed the point in a letter to Hooker, and finished up with the words:—'I would give a guinea if vine-tendrils could be found to be leaves.'³ Later on he discovered a plant with branches possessing the qualities which seemed essential in the forerunners of these sensitive organs, and he wrote

¹ To his daughter, Mrs. Litchfield, Jan. 4, 1875. *Life and Letters*, iii. 202.

² To Sir Lauder Brunton, Feb. 14, 1882. *Ibid.*, 210, also *More Letters*, ii. 441. Edmund Gurney's articles appeared in the *Fortnightly Review*, 1881, xxx. 778, and *Cornhill Magazine*, 1882, xlv. 191.

³ Feb., 1864 (?). *More Letters*, ii. 342.

to the same friend, ‘. . . tell Oliver I now do not care at all how many tendrils he makes axial, which at one time was a cruel torture to me.’¹ Alluding to a hypothesis on the relation between the order of development of parts in the individual and the complexity of its organization, he wrote to Huxley, who had expressed an adverse opinion:—‘I shall, of course, not allude to this subject, which I rather grieve about, as I wished it to be true; but, alas! a scientific man ought to have no wishes, no affections—a mere heart of stone.’² These quotations taken alone would give an utterly wrong impression of Darwin as a scientific man. Two passages will be sufficient to show that his well-balanced mind was secure against the dangers of a too great devotion to the creations of his brilliant imagination. ‘It is a golden rule,’ he wrote to John Scott, ‘which I try to follow, to put every fact which is opposed to one’s preconceived opinion in the strongest light. Absolute accuracy is the hardest merit to attain, and the highest merit. Any deviation is ruin.’³ Again, he wrote in his autobiography in 1881:—

‘I have steadily endeavoured to keep my mind free so as to give up any hypothesis, however much beloved (and I cannot resist forming one on every subject), as soon as facts are shown to be opposed to it. Indeed, I have had no choice but to act in this manner, for with the exception of

¹ June 2, 1864. *More Letters*, ii. 343. ² July 9, 1857. *Ibid.*, i. 98.

³ July 2, 1863 (?). *More Letters*, ii. 324. See also *Life and Letters*, iii. 54, and *ibid.*, i. 87, where Darwin speaks of always making a note of hostile facts.

the Coral Reefs, I cannot remember a single first-formed hypothesis which had not after a time to be given up or greatly modified. This has naturally led me to distrust greatly deductive reasoning in the mixed sciences.’¹

It is impossible on the present occasion to attempt any analysis of Darwin’s genius. I wish, however, to show how clearly he recognized that the love of knowledge for its own sake was the one essential qualification for a scientific man. In his autobiography (1881) he puts ‘the love of science’ first among the qualities to which he owed his success.² But far earlier in his life, when he was under 40, Darwin wrote to his old teacher Henslow :—

‘I rather demur to one sentence of yours—viz., “However delightful any scientific pursuit may be, yet, if it should be wholly unapplied, it is of no more use than building castles in the air.” Would not your hearers infer from this that the practical use of each scientific discovery ought to be immediate and obvious to make it worthy of admiration? What a beautiful instance chloroform is of a discovery made from purely scientific researches, afterwards coming almost by chance into practical use! For myself I would, however, take higher ground, for I believe there exists, and I feel within me, an instinct for truth, or knowledge or discovery, of something of the same nature as the instinct of virtue,

¹ *Life and Letters*, i 103, 104. See also 149, where Mr. Francis Darwin states :—‘It naturally happened that many untenable theories occurred to him; but fortunately his richness of imagination was equalled by his power of judging and condemning the thoughts that occurred to him. He was just to his theories, and did not condemn them unheard . . .’

² *Life and Letters*, i. 107. See also 103, where he says (1881) :—‘What is far more important [than powers of observation, industry, &c.], my love of natural science has been steady and ardent. This pure love has, however, been much aided by the ambition to be esteemed by my fellow naturalists.’

and that our having such an instinct is reason enough for scientific researches without any practical results ever ensuing from them.’¹

The same high motive was expressed in similar language in a letter to his second cousin, W. D. Fox:—

‘You do me injustice when you think that I work for fame; I value it to a certain extent; but, if I know myself, I work from a sort of instinct to try to make out truth.’²

The ‘higher ground’ taken by Darwin is now recognized as the only motive cause which can lead to scientific work at its best. The scientific spirit is essentially and intensely antimaterialist. The expression of an opposite opinion, in spite of the superficial plausibility that made it at one time popular, can only lead in these days to humorous exaggerations such as that contained in the toast said to have been drunk at a Cambridge mathematical society:—‘To the latest discovery in pure mathematics, and may it never be of the slightest use to anybody.’

One other dominant element in Darwin’s genius which has been sometimes forgotten, must be referred to. I mean the power thus described in the autobiography (1881):—

‘. . . I think that I am superior to the common run of men in noticing things which easily escape attention, and in observing them carefully.’³

¹ April 1, 1848 *More Letters*, i. 61.

² Mar. 24, 1859. *Life and Letters*, ii. 150.

³ *Life and Letters*, i. 103. The editors of *More Letters* (i. 72) speak of ‘that supreme power of seeing and thinking what the rest of the world had overlooked, which was one of Darwin’s most striking characteristics’.

In attempting to estimate the position of Darwin in the intellectual history of his country and of the world, I will quote the opinion of one whose interests are literary rather than scientific. Lord Courtney, proposing the toast of 'The Royal Society' at the anniversary dinner a few years ago, compared the scientific with the literary contribution made by the English-speaking nations to the brief list of the world's greatest men. In literature of course there was Shakespeare, but who could be placed as a second? 'Many,' said the speaker, 'would propose Milton. Our continental friends might suggest for us Byron'; but for himself Lord Courtney was inclined to think that Shakespeare stood in that great world-list alone, without an English-speaking rival or even a second. When, however, he turned to science, the speaker expressed his belief that two names must be admitted as our contribution. I accept the opinion and believe that it will be widely accepted. So far as we can estimate such positions and make such comparisons, Newton and Darwin stand together and for all time in the select company of the greatest men the world has ever seen.

III

THE DARWIN CENTENARY AT OXFORD

The Oxford Celebration of the hundredth anniversary of the birth of Charles Darwin, Feb. 12, 1809.

THE hundredth anniversary of the birth of Charles Darwin was celebrated at Oxford on the evening of Feb. 12, 1909, by a reception held in the Examination Schools by Professors S. H. Vines, G. C. Bourne, and E. B. Poulton. The reception was honoured by the presence of four sons of Charles Darwin—Mr. William Erasmus Darwin, Sir George Darwin, Mr. Francis Darwin, and Major Leonard Darwin; as also by that of Professor Judd and Professor Meldola. No attempt was made to extend the commemoration widely beyond the limits of Oxford, but invitations were sent to all the names upon the list of Congregation, and the great anniversary was celebrated, as had been intended, by a large gathering of members of the University. Among these several non-residents were able to be present, including Sir William Thiselton-Dyer, Dr. D. H. Scott, President of the Linnean Society of London, Professor J. B. Farmer, and Dr. P. Chalmers Mitchell.

Mr. Julian Huxley, a grandson of the late Professor Huxley, Mr. H. Moseley, son of the

late Professor H. N. Moseley, Mr. Geoffrey Smith, Mr. R. Bourne, Mr. A. F. Coventry, and Mr. E. P. Poulton acted as stewards.

Special distinction was conferred upon the celebration by the deeply interesting speeches of Sir George Darwin and Mr. Francis Darwin. An address by the present writer was based upon material contained in the two previous addresses, a special point being made of the true interpretation to be placed upon those changes in Darwin's mind, described on pp. 59, 60, which have been so widely and unfortunately misunderstood. It was to the speaker a supreme pleasure to find that the interpretation was entirely accepted by Darwin's sons, and to hear it brought forward in Mr. William Darwin's speech at the Cambridge banquet on June 23rd,—a speech which charmed and delighted every one who had the privilege of listening to it.

There was good and sufficient reason for directing special attention to this point; for on the previous day (Feb. 11) the first and principal article in the Literary Supplement of the *Times*, entitled *Literature and Science*, was devoted to this very subject, repeated the old errors and spoke of them as unquestioned facts. The author referred to

'The unchallenged assumption, so widespread in these days, that science is not truly science unless it is free from all suspicion of poetic exaltation, and that poetry is a place of dreams and divinations which are chilled by the touch of science.'

He considered that we must reckon with

‘the fact that to give the mind full and free play in one direction seems as yet to imply the atrophy of its activities in the other.’

The article was evidently written for the anniversary, and that the visionary antagonism which so unnecessarily distressed the author was founded on the misinterpretation of Darwin’s life is clear from the following passage:—

‘If a man so utterly incapable of taking an intolerant or a contemptuous view of the life of art could yet find that his own work produced in him the decay of all faculty of artistic enjoyment, we have indeed a proof of the extent to which the two temperaments have diverged.’

The author spoke also of the fine intellectual training, conferred by the combined ‘austerity and responsiveness’ of Darwin’s work, as one which nevertheless ‘leaves untouched and undeveloped, positively even starves, the faculty of aesthetic enjoyment’. And he finally touched the high-water mark in these astounding words:—

‘The case of a man given up to scientific investigations, who yet reads Shakespeare without finding him so dull as to be nauseating, is a case which stands out, which is remarked, which is felt to be notable. As long as this is so we must take Darwin’s case to be typical of the rule.’

I will not call this statement an exaggeration, and thus imply that it contains a minute kernel of truth: I unhesitatingly affirm that it is wholly and utterly false. Few can be happier than I in the intimate friendship of scientific men,

—British, American, and Continental,—men following every branch of science ; and yet, with this wide experience, I do not know a single one to whom the author's words could be fairly applied. Speaking for myself, if I may venture upon what, in the circumstances is not a piece of unnecessary egotism, I would gratefully record the refreshment and delight which I have ever found in the works of the English poets. I allude to it, because one who keenly feels this pleasure only too easily detects and is chilled by the want of appreciation of it in others. I should not indeed be surprised if the author's charge against scientific men were true of certain students of literature, men who seem to have triumphed over our conventional tests—in the letter so exacting, so heedless of the spirit—by means of a knack or trick, and emerge victorious without any perceptible trace of refinement or of interest in any subject, even their own. Such men compare unfavourably with one of our greatest professional exponents of the most difficult of all games, who confessed that, although he did not really care for golf, he was devoted to poaching.

In this protest, which I have felt it my duty to make, I do not in any way question the author's good faith. It is evident in every line, while the article, when not concerned with the supposed tastes of scientific men, shows great breadth of view and keen penetration. The extraordinary misstatements are due in the first place to the

common misinterpretation of Darwin's experience, in the second to false assumptions about a class of workers of whom the author evidently knows nothing. His views on the relation between the creative efforts of the imagination in science and in art are true and clear-sighted. They are admirably expressed in the following passage :—

‘Darwin had, of course, like many lesser men, an immense power of observing and storing facts; but that after all concerned merely the preparation of the stage, so to speak, which was thus swept and lighted for his genius to occupy. The work of his genius was, as he put it, to grind out general laws, or, rather, as we may more sympathetically phrase it, to take the sudden imaginative leap, seizing the exact moment which justifies it, from the particular to the general. To that moment all the patient and impartial amassing of evidence was subsidiary. We may see in that moment, when it arrived, a strong appeal to the imagination on one side, met by an immediate response to it on the other. To fix the eye successively upon detail, and at the critical instant to shift the focus so as to embrace the whole mass—that is not a process which implies the suppression of imagination. It is a process which means for the imagination a continual and austere exercise—austere because every vague or unmeaning impulse is forbidden, continual because the mind must be unceasingly alert to catch the moment for its leap. It approaches very near, we surely begin to see, to the process by which, for the artist, a thousand different fragments of perception are transmuted into the single symbolic image which embraces and explains them all.’

It is an unfortunate result of the inevitable specialization of the present day that one who could write so well of science should know absolutely nothing of scientific workers. It is

still more unfortunate that, knowing nothing, he should publish his conclusions about them. And yet scientific men, extreme specialists as they are and must be in their researches, are not without some knowledge of the lives and interests of their literary and artistic comrades.

It is not necessary or desirable to consider here the hypothesis by which the author explains to his own satisfaction an antagonism which only exists in his imagination. But it is right to say a few words about his treatment of science as something essentially modern. The sciences are not new. Aristotle, it has been well said, was just the kind of man one would expect to meet at the Royal Society or in the Athenaeum. But the spirit of science goes back far beyond the days of Aristotle, to the dawning of the love of knowledge in the developing mind of man, to that *primaeval* time when wonder first became mingled with delight as he looked upon the world around him. But the ancient desire to find out the ways of nature is gratified in an inexhaustible field where every fulfilment brings a new desire and fresh territory. For this reason the comradeship of scientific men is both stimulating and encouraging to the followers of literature, poring, as so many of them do, over world-worn themes of matchless dignity and beauty, but breathing all the time an atmosphere which tends to over-develop the purely critical faculties and to leave the creative imagination dwarfed and stunted.

IV

CHARLES DARWIN AND THE UNIVERSITY OF CAMBRIDGE

Revised from the shorthand notes of a speech delivered on June 23rd, 1909, at the Banquet given by the University of Cambridge in honour of the Delegates to the Darwin Celebration.

CHANCELLOR, your Excellencies, my Lords and Gentlemen, it is a proud position to be asked, as a representative of the University of Oxford, to propose, on this memorable occasion, the toast of 'The University of Cambridge'. It is with considerable diffidence that I attempt to fill it.

The greatness of a University may be most truly measured by the greatness of its sons, and by the force of the intellectual movements to which it has given rise. Mr. Balfour has spoken of the mighty names borne by sons of Cambridge. I trust that I shall enlist your sympathy in dwelling for a few moments on the University life of one of the greatest of these, the illustrious man whom we commemorate to-day, and also in attempting very briefly to show how his mature thoughts were received in both the ancient Universities of this country. It was in Cambridge, as you know well, that Charles Darwin

came under the guidance of Professor Henslow, a circumstance which, as he said, influenced his whole career more than any other. To Henslow he owed the possibility of sailing in the *Beagle*, the greatest event, as he believed, in his scientific life—the one event which made all the rest possible.¹ We must also remember how Darwin's interest in geology was aroused by Professor Sedgwick. It was on his return from a geological tour in North Wales with Sedgwick that Darwin found the letter from Henslow, offering him the post on the *Beagle*. However lightly it was regarded by Darwin himself, there can be no doubt of the great depth of his debt to Cambridge.

In thinking over the names of the great men who have sprung from the University of Cambridge, I have been led to reflect on the long harmonious years of sisterhood between our two ancient Universities, to remember how the thoughts that have arisen in the one have been strengthened by resonance in the other, to call to mind the dependence of the greatest of men upon appreciation and sympathy.

Professor H. H. Turner has recently shown that the shy and sensitive genius of Newton, irritated by the correspondence with Hooke, might perhaps have been altogether lost to

¹ 'The voyage of the *Beagle* has been by far the most important event in my life, and has determined my whole career . . . I have always felt that I owe to the voyage the first real training or education of my mind . . .' *Life and Letters*, i. 61.

Science, were it not for the 'immortal journey' to Cambridge made by the Oxford man Halley in August, 1684.

Through the relationship and mutual interdependence between great minds we can also trace the influence of Oxford upon Darwin. Sir Ray Lankester spoke this morning of the debt which Lyell owed to the teaching of Buckland at Oxford, and how similar it was to the debt which Darwin owed to Henslow at Cambridge. But there is the strongest evidence, given in Darwin's own words, that he also owed a deep debt to Lyell, and therefore indirectly to Buckland and Oxford.

The first volume of the first edition of Lyell's *Principles of Geology* came out in 1830, just before Darwin started on the voyage of the *Beagle*. He was advised by Henslow to read it, but on no account to believe the views therein contained; but Darwin was proud to remember that, at the very first opportunity of testing Lyell's reasoning, he recognized the infinite superiority of his teachings over those of all others. Many years later he wrote to L. Horner: 'I always feel as if my books came half out of Lyell's brain I have always thought that the great merit of the *Principles* was that it altered the whole tone of one's mind, and therefore that, when seeing a thing never seen by Lyell, one yet saw it partially through his eyes.'¹

¹ See also pp. 5-7.

When did Darwin acknowledge his debt in this way? It was on Aug. 29th, 1844. In 1842 he had written the first brief account of his theory of evolution—that sketch which will now be for the first time in the hands of the public—that sketch of which, thanks to your generosity, a gift has been made to every guest whom you are welcoming to Cambridge, a work which I for my part look forward to reading with greater pleasure and greater interest than any book I have ever possessed. In 1844 Darwin had further elaborated this sketch into a completed essay which he felt, whatever happened, would contain a sufficient account of his views; and on July 5 he made his ‘solemn and last request’ to his wife, begging her, in the event of his death, to make arrangements for its publication. Only a few weeks after this, the psychological moment in his career, Darwin acknowledged his debt to Lyell; and when we consider how intensely Lyellian were the three lines of argument—two based on geographical distribution, and one on the relation between the most recent fossils and the forms now living in a country—by which Darwin was first convinced of the truth of evolution, we cannot avoid the conclusion that he was right in feeling the debt to be a very heavy one.

Although Darwin spoke of the three years at Cambridge as ‘the most joyful in my happy life’, neither he nor Lyell appear to have thought that

they owed very much to their Universities. In this respect I cannot but believe that both these great men were mistaken, and I think it would be interesting to inquire what would be likely to happen to such men as Darwin or Lyell if they entered Cambridge or Oxford at the present day.

I remember many years ago seeing in the papers among the news from India a message which read, with the quaint humour oftentimes conferred by the abbreviation of telegraphic dispatch: 'A new Saint has appeared in the Northern Provinces. The police are already on his track.' In not dissimilar language we must own that when fresh genius appears at the Universities, the examiners are hard upon its track; and the effect of the pressure of examinations upon genius is apt to be similar to that of the removal of Pharaoh's chariot wheels,—so that they drave heavily. And with regard to Darwin's teacher Henslow, would the Henslow of to-day have the time and the opportunity to discover and to influence a student who did not care to read for Honours, but preferred to go into the country to collect beetles or into the Fens to collect plants? I do not ask these questions in any pessimistic spirit. There is no need for despair; for I believe that we are all aware of the danger of the excessive pressure of examinations at the present moment in both our ancient Universities, and indeed to an even greater extent throughout the whole of the British Empire. Cambridge has

recently made great and important changes precisely in the direction I am indicating—changes tending to relieve this pressure; and we in Oxford have made alterations intended to produce the same effect. I believe we are likely to improve still further in this matter, and, without losing our modern efficiency, regain a greater freedom and greater elasticity, and a freer recognition of unusual powers—in these respects assimilating more closely to the Universities of three-quarters of a century ago.

Turning now to the ancient Universities as the lists where new ideas are compelled to undergo the trial of combat, we observe that the battle of evolution began with the dramatic encounter between Huxley and Wilberforce at the meeting of the British Association at Oxford, in 1860, and, according to Professor Alfred Newton, came to a close with the victory of the new teachings, only two years later, at the meeting of the same Association at Cambridge.

Whatever happened in the great arena furnished by the two ancient Universities, there can be no doubt that for many years neither of them was at all willing to accept the conclusions of Darwin. One of the most strongly antagonistic letters received by Darwin was written by his old teacher, Sedgwick. Whewell kept the *Origin of Species* out of the library at Trinity College for some years; while Professor Westwood seriously proposed to the last Oxford University

Commission the establishment of a permanent lectureship for the exposure of the fallacies of Darwinism.

Charles Darwin was offered the honorary degree of D.C.L. by Lord Salisbury, on his installation as Chancellor of the University of Oxford in 1870. After the lapse of nearly forty years there can be no harm in the candid admission that Lord Salisbury's list was opposed, although unsuccessfully, in the Hebdomadal Council. There is no evidence that any special exception was taken to the name of Darwin, but certain members of Council objected to the high proportion of scientific men. The opposition was unsuccessful, the Chancellor's list was passed as a whole, and became the list of the Council ; but, unfortunately for Oxford, Darwin's health prevented him from accepting the degree. Cambridge was happier, and Darwin became an honorary LL.D. of his own University in 1877.

And now there is one other subject to which I desire to allude before proposing the toast. What would we give to know as much about the life of Shakespeare and of Newton as we know about the life of Darwin ? That we do happily possess a wide and detailed knowledge of the life of this great man we owe to one of his sons, who, with a fine and delicate sense of pathos as well as performance, has done his work, who has hurried in no way but has made every step secure, so that we can with the utmost confidence receive the

great result as historical truth that will stand the test of time—a sure foundation on which the future can build. This great debt we owe. It is difficult to express our gratitude in adequate terms, but I should wish to say on behalf of those of us who are here as guests of the University of Cambridge that we look with a sympathy of the utmost depth upon the majestic ceremony that will take place to-morrow, when you will make the great exception and dignify with an honorary degree a resident Cambridge man.

I give you the toast of the 'University of Cambridge', venerable yet ever young, the mother of great men. And I know that when you honour it you will think of one mighty name, the noble, illustrious name of him through whom Cambridge may not unjustly claim that she has taught and inspired the world

V

THE VALUE OF COLOUR IN THE STRUGGLE FOR LIFE

Essay XV in *Darwin and Modern Science : Essays in commemoration of the centenary of the birth of Charles Darwin and of the fiftieth anniversary of the publication of 'The Origin of Species'*, edited by Prof. A. C. Seward, Cambridge University Press (1909), 271-297. Somewhat extended.

INTRODUCTION.

THE following pages have been written chiefly from the historical standpoint. Their principal object has been to give some account of the impressions produced on the mind of Darwin and his great compeer Wallace by various difficult problems suggested by the colours of living nature. In order to render the brief summary of Darwin's thoughts and opinions on the subject in any way complete, it was found necessary to say again much that has often been said before. No attempt has been made to display as a whole the vast contribution of Wallace ; but certain of its features are incidentally revealed in passages quoted from Darwin's letters. It is assumed that the reader is familiar with the well-known theories of Protective Resemblance, Warning Colours, and Mimicry both Batesian and Mullerian. It would have

been superfluous to explain these on the present occasion; for a far more detailed account than could have been attempted in these pages has recently appeared.¹ Among the older records I have made a point of bringing together the principal observations scattered through the notebooks and collections of W. J. Burchell. These have never hitherto found a place in any memoir dealing with the significance of the colours of animals. A few new observations which seemed to be of special interest have been included, together with some fresh considerations deserving of attention in the study of Mimicry in relation to sex.

INCIDENTAL COLOURS

Darwin fully recognized that the colours of living beings are not necessarily of value as colours, but that they may be an incidental result of chemical or physical structure. Thus he wrote to T. Meehan, Oct. 9, 1874:—

‘I am glad that you are attending to the colours of diœcious flowers; but it is well to remember that their colours may be as unimportant to them as those of a gall, or, indeed, as the colour of an amethyst or ruby is to these gems.’²

Incidental colours remain as available assets of the organism ready to be turned to account by Natural Selection. It is a probable speculation

¹ Poulton, *Essays on Evolution*, Oxford, 1908, 293-382.

² *More Letters*, i. 354, 355. See also the admirable account of incidental colours in *Descent of Man* (2nd edit., 1874), 261, 262.

that all pigmentary colours were originally incidental; but now and for immense periods of time the visible tints of animals have been modified and arranged so as to assist in the struggle with other organisms or in courtship. The dominant colouring of plants, on the other hand, is an essential element in the paramount physiological activity of chlorophyll. In exceptional instances, however, the shapes and visible colours of plants may be modified in order to promote concealment.¹

TELEOLOGY AND ADAPTATION

In the department of Biology, which forms the subject of this essay, the adaptation of means to an end is probably more evident than in any other; and it is therefore of interest to compare, in a brief introductory section, the older with the newer teleological views.

The distinctive feature of Natural Selection as contrasted with other attempts to explain the process of evolution is the part played by the struggle for existence. All naturalists in all ages must have known something of the operations of 'Nature red in tooth and claw'; but it was left for this great theory to suggest that vast extermination is a necessary condition of progress, and even of maintaining the ground already gained.

Realizing that fitness is the outcome of this

¹ See pp. 96-8, 102, 103.

fierce struggle, thus turned to account for the first time, we are sometimes led to associate the recognition of adaptation itself too exclusively with Natural Selection. Adaptation had been studied with the warmest enthusiasm nearly forty years before this great theory was given to the scientific world, and it is difficult now to realize the impetus which the works of Paley gave to the study of Natural History. That they did inspire the naturalists of the early part of the last century is clearly shown in the following passages.

In the year 1824 the Ashmolean Museum at Oxford was entrusted to the care of J. S. Duncan of New College. He was succeeded in this office by his brother, P. B. Duncan, of the same College, author of a history of the Museum, which shows very clearly the influence of Paley upon the study of nature, and the dominant position given to his teachings: 'Happily at this time [1824] a taste for the study of natural history had been excited in the University by Dr. Paley's very interesting work on Natural Theology, and the very popular lectures of Dr. Kidd on Comparative Anatomy, and Dr. Buckland on Geology.' In the arrangement of the contents of the Museum the illustration of Paley's work was given the foremost place by J. S. Duncan :—

'The first division proposes to familiarize the eye to those relations of all natural objects which form the basis of argument in Dr. Paley's Natural Theology ; to induce a mental habit of associating the view of natural phenomena with the conviction that they are the media of Divine manifestation ;

and by such association to give proper dignity to every branch of natural science.’¹

The great naturalist, W. J. Burchell, in his classical work shows the same recognition of adaptation in nature at a still earlier date. Upon the subject of collections he wrote² :—

‘It must not be supposed that these charms [the pleasures of Nature] are produced by the mere discovery of new objects: it is the harmony with which they have been adapted by the Creator to each other, and to the situations in which they are found, which delights the observer in countries where Art has not yet introduced her discords.’

The remainder of the passage is so admirable that I venture to quote it :—

‘To him who is satisfied with amassing collections of curious objects, simply for the pleasure of possessing them, such objects can afford, at best, but a childish gratification, faint and fleeting; while he who extends his view beyond the narrow field of nomenclature, beholds a boundless expanse, the exploring of which is worthy of the philosopher, and of the best talents of a reasonable being.’

On Sept. 14, 1811, Burchell was at Zand Valley (Vlei), or Sand Pool, a few miles south-west of the site of Prieska, on the Orange River. Here he found a *Mesembryanthemum* (*M. turbiniforme*, now *M. truncatum*) and also a *Gryllus* (Acridian), closely resembling the pebbles with which their locality was strewn. He says of both of these,

¹ From *History and Arrangement of the Ashmolean Museum*, by P. B. Duncan, *A Catalogue of the Ashmolean Museum*, Oxford, (1836), vi, vii.

² *Travels in the Interior of Southern Africa*, London, i. (1822), 505. The references to Burchell's observations in the present essay are adapted from the author's article in *Report of the British and South African Associations*, 1905, in. 57–110.

'The intention of Nature, in these instances, seems to have been the same as when she gave to the Chameleon the power of accommodating its color, in a certain degree, to that of the object nearest to it, in order to compensate for the deficiency of its locomotive powers. By their form and color, this insect may pass unobserved by those birds, which otherwise would soon extirpate a species so little able to elude its pursuers, and this juicy little *Mesembryanthemum* may generally escape the notice of cattle and wild animals.' ¹

Burchell here seems to miss, at least in part, the meaning of the relationship between the quiescence of the Acridian and its cryptic colouring. It is a relationship of co-operation rather than compensation; for quiescence is an essential element in the protective resemblance to a stone—probably even more indispensable than the details of the form and colouring. Furthermore, the chameleon can make certain movements quickly enough when occasion requires. My friend Professor Lloyd Morgan has seen an African chameleon, when a snake was brought near it, instantaneously quit its hold of the branch, draw in its legs, and fall like a stone to the ground. Although Burchell appears to overlook this point

¹ Ibid., 310, 311. See Sir William Thiselton-Dyer, 'Morphological Notes,' xi.; 'Protective Adaptations,' 1.; *Annals of Botany*, xx, 124. In plates vii. viii. and ix. accompanying this article, the author represents the species observed by Burchell, together with others in which analogous adaptations exist. He writes: 'Burchell was clearly on the track on which Darwin reached the goal. But the time had not come for emancipation from the old teleology. This, however, in no respect detracts from the merit or value of his work. For, as Huxley has pointed out (*Huxley's Life and Letters*, 1900, i. 457), the facts of the old teleology are immediately transferable to Darwinism, which simply supplies them with a natural in place of a supernatural explanation.'

he fully recognized the community between protection by concealment and more aggressive modes of defence; for, in the passage of which a part is quoted above, he specially refers to some earlier remarks on p. 226 of his vol. i. We here find that when the oxen were resting by the Juk rivier (Yoke river), on July 19, 1811, Burchell observed '*Geranium spinosum*, with a fleshy stem and large white flowers . . .; and a succulent species of *Pelargonium* . . . so defended by the old panicles, grown to hard woody thorns, that no cattle could browse upon it.' He goes on to say, 'In this arid country, where every juicy vegetable would soon be eaten up by the wild animals, the Great Creating Power, with all-provident wisdom, has given to such plants either an acrid or poisonous juice, or sharp thorns, to preserve the species from annihilation . . .' All these modes of defence, especially adapted to a desert environment, have since been generally recognized, and it is very interesting to place beside Burchell's statement the following passage from a letter written by Darwin, Aug. 7, 1868, to G. H. Lewes:—

'That Natural Selection would tend to produce the most formidable thorns will be admitted by every one who has observed the distribution in South America and Africa (*vide* Livingstone) of thorn-bearing plants, for they always appear where the bushes grow isolated and are exposed to the attacks of mammals. Even in England it has been noticed that all spine-bearing and sting-bearing plants are palatable to quadrupeds, when the thorns are crushed.'¹

¹ *More Letters*, i. 308.

ADAPTATION AND NATURAL SELECTION

I have preferred to show the influence of the older teleology upon Natural History by quotations from a single great and insufficiently appreciated naturalist. It might have been seen equally well in the pages of Kirby and Spence and those of many other writers. If the older naturalists who thought and spoke with Burchell of 'the intention of Nature' and the adaptation of beings 'to each other, and to the situations in which they are found', could have conceived the possibility of evolution, they must have been led, as Darwin was, by the same considerations, to Natural Selection. This was impossible for them, because the philosophy which they followed contemplated the phenomena of adaptation as part of a static immutable system. Darwin, convinced that the system is dynamic and mutable, was prevented by these very phenomena from accepting anything short of the crowning interpretation offered by Natural Selection.¹ And the birth of Darwin's unalterable conviction that adaptation is of dominant importance in the organic world,—a conviction confirmed and ever again confirmed by his experience as a naturalist—may probably be traced to the in-

¹ 'I had always been much struck by such adaptations [e.g. woodpecker and tree-frog for climbing, seeds for dispersal], and until these could be explained it seemed to me almost useless to endeavour to prove by indirect evidence that species have been modified.' Autobiography in *Life and Letters*, i. 82. The same thought is repeated again and again in Darwin's letters to his friends. It is forcibly urged in the Introduction to the *Origin* (1859), 3.

fluence of the great theologian. Thus Darwin, speaking of his Undergraduate days, tells us in his Autobiography that the logic of Paley's *Evidences of Christianity* and *Moral Philosophy* gave him as much delight as did Euclid.

'The careful study of these works, without attempting to learn any part by rote, was the only part of the academical course which, as I then felt and as I still believe, was of the least use to me in the education of my mind. I did not at that time trouble myself about Paley's premises; and taking these on trust, I was charmed and convinced by the long line of argumentation.'¹

When Darwin came to write the *Origin* he quoted in relation to Natural Selection one of Paley's conclusions. 'No organ will be formed, as Paley has remarked, for the purpose of causing pain or for doing an injury to its possessor.'²

The study of adaptation always had for Darwin, as it has for many, a peculiar charm. His words, written Nov. 28, 1880, to Sir W. Thiselton-Dyer, are by no means inappropriate at the present day, nor is their application by any means to be restricted to a single nation: 'Many of the Germans are very contemptuous about making out use of organs; but they may sneer the souls out of their bodies, and I for one shall think it the most interesting part of natural history.'³

Mr. Francis Darwin truly says:—

'One of the greatest services rendered by my father to the

¹ *Life and Letters*, i. 47.

² *Origin of Species* (1st edit.), 1859, 201.

³ *More Letters*, ii. 428.

study of Natural History is the revival of Teleology. The evolutionist studies the purpose or meaning of organs with the zeal of the older Teleology, but with far wider and more coherent purpose.'¹

PROTECTIVE AND AGGRESSIVE RESEMBLANCE: PROCRYPTIC AND ANTICRYPTIC COLOURING

Colouring for the purpose of concealment is sometimes included under the head Mimicry, a classification adopted by H. W. Bates in his classical paper. Such an arrangement is inconvenient, and I have followed Wallace in keeping the two categories distinct.

The visible colours of animals are far more commonly adapted for Protective Resemblance than for any other purpose. The concealment of animals by their colours, shapes and attitudes, must have been well known from the period at which human beings first began to take an intelligent interest in Nature. An interesting early record is that of Samuel Felton, F.R.S., who (Dec. 2, 1763) figured and gave some account of an Acridian (*Phyllotettix*) from Jamaica. Of this insect he says '*the thorax is like a leaf that is raised perpendicularly from the body*'.²

Both Protective and Aggressive Resemblances were appreciated and clearly explained by Erasmus Darwin in 1794: 'The colours of many animals seem adapted to their purposes

¹ *Life and Letters*, iii. 255.

² *Phil. Trans. Roy. Soc.*, lv. Tab. vi. 55.

of concealing themselves either to avoid danger, or to spring upon their prey.'¹

Protective Resemblance of a very marked and beautiful kind is found in certain plants inhabiting desert areas. Examples observed by Burchell almost exactly a hundred years ago have already been mentioned on pp. 96-8. In addition to the resemblance to stones Burchell observed, although he did not publish the fact, a South African plant concealed by its likeness to the dung of birds.² The observation is recorded in one of the manuscript journals kept by the great explorer during his journey. I owe the opportunity of studying it to the kindness of Mr. Francis A. Burchell of the Rhodes University College, Grahamstown. The following account is given under the date July 5, 1812, when Burchell was at the Makkwárin River, about half-way between the Kuruman River and Litakun the old capital of the Bachapins (Bechuanas):—

'I found a curious little *Crassula* (not in flower) so snow white, that I should never has [have] distinguished it from the white limestones. . . . It was an inch high and a little

¹ *Zoonomia*, i London, 1794, 509

² Sir William Thiseleton-Dyer has suggested the same method of concealment (*Annals of Botany*, xx. 123) Referring to *Anacampses papyracea*, figured on plate ix, the author says of its adaptive resemblance. 'At the risk of suggesting one perhaps somewhat far-fetched, I must confess that the aspect of the plant always calls to my mind the dejecta of some bird, and the more so owing to the whitening of the branches towards the tips' (ibid, 126). The student of insects, who is so familiar with this very form of protective resemblance in larvae, and even perfect insects, will not be inclined to consider the suggestion far-fetched.

branchy, . . . and was at first mistaken for the dung of birds of the passerine order. I have often had occasion to remark that in stony place[s] there grow many small succulent plants and abound insects (chiefly Grylli) which have exactly the same color as the ground and must for ever escape observation unless a person sit on the ground and observe very attentively.'

The cryptic resemblances of animals impressed Darwin and Wallace in very different degrees, probably in part due to the fact that Wallace's tropical experiences were so largely derived from the insect world, in part to the importance assigned by Darwin to Sexual Selection, 'a subject which had always greatly interested me,' as he says in his Autobiography.¹ There is no reference to Cryptic Resemblance in Darwin's section of the Joint Essay, although he gives an excellent short account of Sexual Selection (see pp. 139, 140). Wallace's section on the other hand contains the following statement:—

'Even the peculiar colours of many animals, especially insects, so closely resembling the soil or the leaves or the trunks on which they habitually reside, are explained on the same principle; for though in the course of ages varieties of many tints may have occurred, *yet those races having colours best adapted to concealment from their enemies would inevitably survive the longest.*'²

It would occupy too much space to attempt any discussion of the difference between the views of

¹ *Life and Letters*, i 94.

² *Journ. Proc. Linn. Soc*, iii. 1859, 61. The italics are Wallace's.

these two naturalists, but it is clear that Darwin, although fully believing in the efficiency of Protective Resemblance and replying to St. George Mivart's contention that Natural Selection was incompetent to produce it,¹ never entirely agreed with Wallace's estimate of its importance. Thus the following extract from a letter to Sir Joseph Hooker, May 21, 1868, refers to Wallace: 'I find I must (and I always distrust myself when I differ from him) separate rather widely from him all about birds' nests and protection; he is riding that hobby to death.'² It is clear from the account given in *The Descent of Man*,³ that the divergence was due to the fact that Darwin ascribed more importance to Sexual Selection than did Wallace, and Wallace more importance to Protective Resemblance than Darwin. Thus Darwin wrote to Wallace, Oct. 12 and 13, 1867: 'By the way, I cannot but think that you push protection too far in some cases, as with the stripes on the tiger.'⁴ Here too Darwin was preferring the explanation offered by Sexual Selection,⁵ a preference which, considering the relation of the colouring of the lion and tiger to their respective environments, few naturalists will be found to share. It is also shown on

¹ *Origin* (6th edit.), London, 1872, 181, 182. See also 66

² *More Letters*, 1 304

³ London, 1874, 452-8. See also *Life and Letters*, III. 123-5, and *More Letters*, II. 59-63, 72-4, 76-8, 84-90, 92, 93.

⁴ *More Letters*, 1 283

⁵ *Descent of Man* (2nd edit.), 1874, 545, 546.

p. 127 that Darwin contemplated the possibility of cryptic colours, such as those of Patagonian animals, being due to Sexual Selection influenced by the aspect of surrounding nature.

Nearly a year later Darwin in his letter of May 5, 1868?, expressed his agreement with Wallace's views: 'Except that I should put sexual selection as an equal, or perhaps as even a more important agent in giving colour than Natural Selection for protection.'¹ The conclusion expressed in the above quoted passage is opposed by the extraordinary development of Protective Resemblance in the immature stages of animals, especially insects.

It must not be supposed, however, that Darwin ascribed an unimportant rôle to Cryptic Resemblances, and as observations accumulated he came to recognize their efficiency in fresh groups of the animal kingdom. Thus he wrote to Wallace May 5, 1867: 'Hackel has recently well shown that the transparency and absence of colour in the lower oceanic animals, belonging to the most different classes, may be well accounted for on the principle of protection.'² Darwin also admitted the justice of Professor E. S. Morse's contention that the shells of molluscs are often adaptively coloured.³ But he looked upon cryptic colouring and also Mimicry as more especially Wallace's departments, and sent to him and to

¹ *More Letters*, ii. 77, 78.

² *More Letters*, ii. 62. See also *Descent of Man* (1874), 261.

³ *More Letters*, ii. 95.

Professor Meldola observations and notes bearing upon these subjects. Thus the following letter given to me by Dr. A. R. Wallace, and now, by kind permission, published for the first time, accompanied a photograph of the chrysalis of *Papilio sarpedon choredon*, Feld., suspended from a leaf of its food-plant:—

July 9th

DOWN,

BECKENHAM, KENT.

MY DEAR WALLACE

Dr. G. Krefft has sent me the enclosed from Sydney. A nurseryman saw a caterpillar feeding on a plant and covered the whole up, but when he searched for the cocoon [pupa], was long before he c^d find it, so good was its imitation in colour and form to the leaf to which it was attached. I hope that the world goes well with you.—Do not trouble yourself by acknowledging this,

Ever yours

CH. DARWIN.

Another deeply interesting letter of Darwin's, bearing upon Protective Resemblance, has only recently been shown to me by my friend Professor E. B. Wilson, the great American Cytologist. With his kind consent and that of Mr. Francis Darwin, this letter, written four months before Darwin's death on April 19, 1882, is reproduced here ¹ :—

¹ The letter is addressed. 'Edmund B Wilson, Esq., Assistant in Biology, John[s] Hopkins University, Baltimore Md., U. States.'

December 21, 1881.

DOWN,
BECKENHAM, KENT.
(Railway Station,
Orpington, S.E.R.)

DEAR SIR,

I thank you much for having taken so much trouble in describing fully your interesting and curious case of mimickry.

I am in the habit of looking through many scientific Journals, and though my memory is now not nearly so good as it was, I feel pretty sure that no such case as yours has been described (amongst the nudibranch) molluscs. You perhaps know the case of a fish allied to *Hippocampus* (described some years ago by Dr. Gunther in *Proc. Zoolog. Soc.*) which clings by its tail to sea-weeds, and is covered with waving filaments so as itself to look like a piece of the same sea-weed. The parallelism between your and Dr. Günther's case makes both of them the more interesting; considering how far a fish and a mollusc stand apart. It w^d be difficult for anyone to explain such cases by the direct action of the environment.—I am glad that you intend to make further observations on this mollusc, and I hope that you will give a figure and if possible a coloured figure.—With all good wishes from an old brother naturalist.

I remain,

Dear Sir,

Yours faithfully,

CHARLES DARWIN.

Professor E. B. Wilson has kindly given the following account of the circumstances under which he had written to Darwin:—

‘The case to which Darwin's letter refers is that of the nudibranch mollusc *Scyllaca*, which lives on the floating *Sargassum* and shows a really astonishing resemblance to the plant, having leaf-shaped processes very closely similar

to the fronds of the sea-weed both in shape and in color. The concealment of the animal may be judged from the fact that we found the animal quite by accident on a piece of *Sargassum* that had been in a glass jar in the laboratory for some time, and had been closely examined in the search for hydroids and the like without disclosing the presence upon it of two large specimens of the *Scyllaea* (the animal, as I recall it, is about two inches long). It was first detected by its movements alone, by someone (I think a casual visitor to the laboratory) who was looking closely at the *Sargassum* and exclaimed, "Why, the sea-weed is moving its leaves!" We found the example in the summer of 1880 or 1881 at Beaufort, N.C., where the Johns Hopkins laboratory was located for the time being. It must have been seen by many others, before or since.

'I wrote and sent to Darwin a short description of the case at the suggestion of Brooks, with whom I was at the time a student. I was, of course, entirely unknown to Darwin (or to anyone else) and to me the principal interest of Darwin's letter is the evidence that it gives of his extraordinary kindness and friendliness towards an obscure youngster who had of course absolutely no claim upon his time or attention. The little incident made an indelible impression upon my memory and taught me a lesson that was worth learning.'

VARIABLE PROTECTIVE RESEMBLANCE

The wonderful power of rapid colour adjustment possessed by the cuttle-fish was observed by Darwin in 1832 at St. Jago, Cape de Verd Islands, the first place visited during the voyage of the *Beagle*. From Rio he wrote to Henslow, giving the following account of his observations, May 18, 1832 :—

'I took several specimens of an Octopus which possessed a most marvellous power of changing its colours, equalling

any chameleon, and evidently accommodating the changes to the colour of the ground which it passed over. Yellowish green, dark brown, and red, were the prevailing colours; this fact appears to be new, as far as I can find out.' ¹

Darwin was well aware of the power of individual colour adjustment now known to be possessed by large numbers of Lepidopterous pupae and larvae. An excellent example was brought to his notice by C. V. Riley,² while the most striking of the early results obtained with the pupae of butterflies—those of Mrs. M. E. Barber upon *Papilio nireus*—was communicated by him to the Entomological Society of London.³

Before leaving the subject of Protective Resemblance I wish to take the opportunity of referring to an observation on the chameleon, read by J. S. Beuttler, Nov. 1, 1873, before the Rugby School Natural History Society and published in the Reports for that date. In this paper the author remarks, 'The side of the animal nearest the light is invariably the darkest.' The same fact was observed in South Africa (1905) by Dr. G. B. Longstaff, who kindly supplied the above quotation, Professor C. V. Boys and the present writer. An interpretation of the later observation was sought along the lines of A. H. Thayer's classical explanation of the white under surfaces of animals, and the conclusion

¹ *Life and Letters*, i. 235, 236. See also the *Journal of Researches*, 1876, 6-8, where a far more detailed account is given, together with a reference to *Encycl. of Anat. and Physiol.*

² *More Letters*, ii. 385, 386.

³ *Trans. Ent. Soc. Lond.*, 1874, 519. See also *More Letters*, ii. 403.

was reached that the colour differences on the two sides neutralize the differences in illumination, and remove the appearance of solidity.¹

It is also necessary to direct attention to C. W. Beebe's² recent discovery that the pigmentation of the plumage of certain birds is increased by confinement in a superhumid atmosphere. In *Scardafella inca*, on which the most complete series of experiments was made, the changes took place only at the moults, whether normal and annual or artificially induced at shorter periods. There was a corresponding increase in the choroidal pigment of the eye. At a certain advanced stage of feather pigmentation a brilliant iridescent bronze or green tint made its appearance on those areas where iridescence most often occurs in allied genera. Thus in birds no less than in insects, characters previously regarded as of taxonomic value, can be evoked or withheld by the forces of the environment.

WARNING OR APOSEMATIC COLOURS

From Darwin's description of the colours and habits it is evident that he observed, in 1833, an excellent example of warning colouring in a little South American toad (*Phryniscus nigricans*). He described it in a letter to Henslow, written

¹ *Zool Journ. Linn Soc.*, xxx. 45.

² *Zoologica: N.Y. Zool Soc.*, 1 No 1, Sept 25, 1907. *Geographic variation in birds with especial reference to the effects of humidity*

from Monte Video, Nov. 24, 1832: 'As for one little toad, I hope it may be new, that it may be christened "diabolicus". Milton must allude to this very individual when he talks of "squat like a toad"; its colours are by Werner [*Nomenclature of Colours*, 1821] ink black, vermilion red and buff orange.'¹ In the *Journal of Researches*² its colours are described as follows: 'If we imagine, first, that it had been steeped in the blackest ink, and then, when dry, allowed to crawl over a board, freshly painted with the brightest vermilion, so as to colour the soles of its feet and parts of its stomach, a good idea of its appearance will be gained.' 'Instead of being nocturnal in its habits, as other toads are, and living in damp obscure recesses, it crawls during the heat of the day about the dry sand-hillocks and arid plains, . . . ' The appearance and habits recall T. Belt's well-known description of the conspicuous little Nicaraguan frog which he found to be distasteful to a duck.³

The recognition of the Warning Colours of caterpillars is due in the first instance to Darwin, who, reflecting on Sexual Selection, was puzzled by the splendid colours of sexually immature organisms. He applied to Wallace, 'who has an innate genius for solving difficulties.'⁴ Darwin's

¹ *More Letters*, i. 12.

² 1876, 97.

³ *The Naturalist in Nicaragua* (2nd edit.), London, 1888, 321.

⁴ *Descent of Man*, 325. On this and the following page an excellent account of the discovery will be found, as well as in Wallace's *Natural Selection*, 1875, 117-22.

original letter exists,¹ and in it we are told that he had taken the advice given by Bates: 'You had better ask Wallace.' After some consideration Wallace replied that he believed the colours of conspicuous caterpillars and perfect insects were a warning of distastefulness and that such forms would be refused by birds. Darwin's reply² is extremely interesting both for its enthusiasm at the brilliancy of the hypothesis and its caution in acceptance without full confirmation:—

'Bates was quite right; you are the man to apply to in a difficulty. I never heard anything more ingenious than your suggestion, and I hope you may be able to prove it true. That is a splendid fact about the white moths;³ it warms one's very blood to see a theory thus almost proved to be true.'

Two years later the hypothesis was proved to hold for caterpillars of many kinds by J. Jenner Weir and A. G. Butler, whose observations have since been abundantly confirmed by many naturalists. Darwin wrote to Jenner Weir, May 13, 1869: 'Your verification of Wallace's suggestion seems to me to amount to quite a discovery.'⁴

RECOGNITION OR EPISEMATIC CHARACTERS

This principle does not appear to have been in any way foreseen by Darwin, although he draws special attention to several elements of pattern

¹ *Life and Letters*, iii 93, 94.

² *Life and Letters*, iii 94, 95.

³ A single white moth which was rejected by young turkeys, while other moths were greedily devoured, *Natural Selection*, 1875, 78.

⁴ *More Letters*, ii. 71 (footnote).

which would now be interpreted by many naturalists as episemes. He believed that the markings in question interfered with the cryptic effect, and came to the conclusion that, even when common to both sexes, they 'are the result of sexual selection primarily applied to the male'.¹ The most familiar of all recognition characters was carefully described by him, although here too explained as an ornamental feature now equally transmitted to both sexes: 'The hare on her form is a familiar instance of concealment through colour; yet this principle partly fails in a closely-allied species, the rabbit, for when running to its burrow, it is made conspicuous to the sportsman, and no doubt to all beasts of prey, by its upturned white tail.'²

The analogous episematic use of the bright colours of flowers to attract insects for effecting cross-fertilization and of fruits to attract vertebrates for effecting dispersal is very clearly explained in the *Origin*.³

It is not, at this point, necessary to treat sematic characters at any greater length. They will form the subject of a large part of the following section, where the models of Batesian (Pseudaposematic) Mimicry are considered as well as the Mullerian (Synaposematic) combinations of Warning Colours.

¹ *Descent of Man*, 544.

² *Descent of Man*, 542.

³ Ed. 1872, 161. For a good example of Darwin's caution in dealing with exceptions see the allusion to brightly coloured fruit in *More Letters*, ii. 348.

MIMICRY—BATESIAN OR PSEUDAPOSEMATIC,
MULLERIAN OR SYNAPOSEMATIC

The existence of superficial resemblances between animals of various degrees of affinity must have been observed for hundreds of years. Among the early examples, the best known to me have been found in the manuscript notebooks and collections of W. J. Burchell, the great traveller in Africa (1810-15) and Brazil (1825-30). The most interesting of his records on this subject are brought together in the following paragraphs.

Conspicuous among well-defended insects are the dark steely or iridescent greenish blue fossorial wasps or sand-wasps, *Sphex* and the allied genera. Many Longicorn beetles mimic these in colour, slender shape of body and limbs, rapid movements, and the readiness with which they take to flight. On Dec. 21, 1812, Burchell captured one such beetle (*Promeces viridis*) at Kosi Fountain on the journey from the source of the Kuruman River to Klaarwater. It is correctly placed among the Longicorns in his catalogue, but opposite to its number is the comment '*Sphex! totus purpureus*'.

In our own country the black-and-yellow colouring of many stinging insects, especially the ordinary wasps, affords perhaps the commonest model for Mimicry. It is reproduced with more or less accuracy on moths, flies and beetles. Among the latter it is again a Longicorn which

offers one of the best-known, although by no means one of the most perfect, examples. The appearance of the well-known 'wasp-beetle' (*Clytus arietis*) in the living state is sufficiently suggestive to prevent the great majority of people from touching it. The dead specimen is less convincing, and when I showed a painting of it to Dr. Alfred Russel Wallace in 1889 he doubted whether it was an example of Mimicry at all. I replied that he would not question the interpretation if he had noticed the beetle in life; and he at once recalled the movements of allied forms in the Eastern Archipelago, and admitted the mimetic resemblance. In fact, the slender, wasp-like legs of the beetle are moved in a rapid, somewhat jerky manner, very different from the usual stolid coleopterous stride, but remarkably like the active movements of a wasp, which always seem to imply the perfection of training.¹ In Burchell's Brazilian collection there is a nearly allied species (*Neoclytus curvatus*) which appears to be somewhat less wasp-like than the British beetle. The specimen bears the number '1188', and the date March 27, 1827, when Burchell was collecting in the neighbourhood of St. Paulo. Turning to the corresponding number in the Brazilian notebook we find this record: 'It runs rapidly like an ichneumon or wasp, of which it has the appearance.'

The formidable, well-defended ants are as freely

¹ Poulton, *The Colours of Animals*, London, 1890, 249, 250.

mimicked by other insects as the sand-wasps, ordinary wasps and bees. Thus on Feb. 17, 1901, Guy A. K. Marshall captured, near Salisbury, Mashonaland, three similar species of ants (Hymenoptera) with a bug (Hemiptera) and a Locustid (Orthoptera), the two latter mimicking the former. All the insects, seven in number, were caught on a single plant, a small bushy vetch.¹

This is an interesting recent example from South Africa, and large numbers of others might be added—the observations of many naturalists in many lands; but nearly all of them known since that general awakening of interest in the subject which was inspired by the great hypotheses of H. W. Bates and Fritz Muller. We find, however, that Burchell had more than once recorded the mimetic resemblance to ants. An extremely ant-like bug (the larva of a species of *Alydus*) in his Brazilian collection is labelled '1141', with the date Dec. 8, 1826, when Burchell was at the Rio das Pedras, Cubatão, near Santos. In the notebook the record is as follows: '1141 *Cimex*. I collected this for a Formica.'

Some of the chief mimics of ants are the active little hunting spiders belonging to the family *Attidae*. Many examples have been brought forward during recent years, especially by my friends Dr. and Mrs. Peckham, of Milwaukee, the great authorities on this group of Arachnids. Here too

¹ *Trans. Ent. Soc. Lond.*, 1902, 535, plate xix, figs. 53-9.

we find an observation of the mimetic resemblance recorded by Burchell, and one which adds in the most interesting manner to our knowledge of the subject. A fragment, all that is now left, of an *Attid* spider, captured on June 30, 1828, at Goyaz, Brazil, bears the following note, in this case on the specimen and not in the notebook: 'Black . . . runs and seems like an ant with large extended jaws.' My friend Mr. R. I. Pocock, to whom I have submitted the specimen, tells me that it is not one of the group of species hitherto regarded as ant-like, and he adds, 'It is most interesting that Burchell should have noticed the resemblance to an ant in its movements. This suggests that the perfect imitation in shape, as well as in movement, seen in many species was started in forms of an appropriate size and colour by the mimicry of movement alone.' Up to the present time Burchell is the only naturalist who has observed an example which still exhibits this ancestral stage in the evolution of mimetic likeness.

Following the teachings of his day, Burchell was driven to believe that it was part of the fixed and inexorable scheme of things that these strange superficial resemblances existed. Thus, when he found other examples of Hemipterous mimics, including one (*Lutera macrophthalma*) with 'exactly the manners of a Mantis', he added the sentence, 'In the genus *Cimex* (Linn.) are to be found the outward resemblances of insects of many other

genera and orders,' Feb. 15, 1829. Of another Brazilian bug, which is not to be found in his collection, and cannot therefore be precisely identified, he wrote: '*Cimex* . . . Nature seems to have intended it to imitate a *Sphex*, both in colour and the rapid palpitating and movement of the antennae,' Nov. 15, 1826. At the same time it is impossible not to feel the conviction that Burchell felt the advantage of a likeness to stinging insects and to aggressive ants, just as he recognized the benefits conferred on desert plants by spines and by concealment (see pp. 96-8). Such an interpretation of Mimicry was perfectly consistent with the theological doctrines of his day.¹

The last note I have selected from Burchell's manuscript refers to one of the chief mimics of the highly protected Lycid beetles. The whole assemblage of African insects with a Lycoid colouring forms a most important combination and one which has an interesting bearing upon the theories of Bates and Fritz Müller. This most wonderful set of mimetic forms, described in 1902 by Guy A. K. Marshall, is composed of flower-haunting beetles belonging to the family *Lycidae*, and the heterogeneous series of varied insects which mimic their conspicuous and simple scheme of colouring. The Lycid beetles, forming the centre or 'models' of the whole company, are orange-brown in front for about two-thirds of the

¹ See Kirby and Spence, *An Introduction to Entomology* (1st edit.), London, n. 1817, 223

exposed surface, black behind for the remaining third. They are undoubtedly protected by qualities which make them excessively unpalatable to the bulk of insect-eating animals. Some experimental proof of this has been obtained by Mr. Guy Marshall. What are the forms which surround them? According to the hypothesis of Bates they would be, at any rate mainly, palatable hard-pressed insects which only hold their own in the struggle for life by a fraudulent imitation of the trade-mark of the successful and powerful *Lycidae*. According to Fritz Müller's hypothesis we should expect that the mimickers would be highly protected, successful and abundant species, which (metaphorically speaking) have found it to their advantage to possess an advertisement, a danger-signal, in common with each other, and in common with the beetles in the centre of the group. According to the first view the mimic is a danger to its model, according to the second it is a benefit. If A, B, C, D, &c., are all unpalatable and all recognized by the same appearance, and if their enemies have to learn by experience what to eat and what to reject, it follows that when A is tasted and found unpleasant, B, C, D, &c., are benefited. They would be tasted more cautiously, or perhaps abandoned without tasting. On the next occasion B might be tasted by some other inexperienced foe, and the advantage would lie with A as well as C, D, &c. It is hardly necessary to explain that under

either hypothesis volition has nothing to do with the growth of resemblance, but that it is believed to be brought about by the survival in successive generations of those individuals most like the model or most like one another. The death of individual A or B as a result of the tasting is no difficulty. Far more individuals of A, B, C, D, &c., would be killed by experimental tasting if they had different patterns than if they had the same, and this is advantage enough to cause a strong trend in the direction of resemblance.

How far does the constitution of this wonderful combination—the largest and most complicated as yet known in all the world—convey to us the idea of Mimicry working along the lines supposed by Bates or those suggested by Müller? Figures 1 to 52 of Mr. Marshall's coloured plate¹ represent a set of forty-two or forty-three species or forms of insects captured in Mashonaland, and all except two in the neighbourhood of Salisbury. The combination includes six species of *Lycidae*; nine beetles of five groups all specially protected by nauseous qualities, *Telephoridae*, *Melyridae*, *Phytophaga*, *Lagriidae*, *Cantharidae*; six Longicorn beetles; one Coprid beetle; eight stinging Hymenoptera; three or four parasitic Hymenoptera (*Braconidae*, a group much mimicked and shown by some experiments to be distasteful); five bugs (Hemiptera, another group in which unpalata-

¹ *Trans. Ent. Soc. Lond.*, 1902, plate xviii. See also 517, where the group is analysed

bility is widespread); three moths (*Arctiidae* and *Zygaenidae*, distasteful families); one fly. In fact the whole combination, except perhaps one Phytophagous, one Coprid and the Longicorn beetles, and the fly, fall under the hypothesis of Müller and not under that of Bates. And it is very doubtful whether these exceptions will be sustained: indeed the suspicion of unpalatability already besets the mimetic Longicorns, and is always on the heels—I should say the hind tarsi—of a Phytophagous beetle.

This most remarkable example which illustrates so well the problem of Mimicry and the alternative hypotheses proposed for its solution, was, as I have said, first described in 1902. Among the most perfect of the mimetic resemblances in it is that between the Longicorn beetle, *Amphidesmus analis*, and the *Lycidae*. It was with the utmost astonishment and pleasure that I found this very resemblance had almost certainly been observed by Burchell. A specimen of the *Amphidesmus* exists in his collection and it bears '651'. Turning to the same number in the African catalogue we find that the beetle is correctly placed among the Longicorns, that it was captured at Uitenhage on Nov. 18, 1813, and that it was found associated with Lycid beetles in flowers ('consocians cum Lycis 78-87 in floribus'). Looking up Nos. 78-87 in the collection and catalogue, three species of *Lycidae* are found, all captured on Nov. 18, 1813, at Uitenhage. Bur-

chell recognized the wide difference in affinity, shown by the distance between the respective numbers : for his catalogue is arranged to represent relationships. He observed, what students of Mimicry are only just beginning to record precisely and systematically, the coincidence between model and mimic in time and space and in habits. We are justified in concluding that he observed the close superficial likeness, although he does not in this case expressly allude to it.

One of the most interesting among the early observations of superficial resemblance between forms remote in the scale of classification was made by Darwin himself, as described in the following passage from his letter to Henslow, written from Monte Video, Aug. 15, 1832:—

‘Amongst the lower animals nothing has so much interested me as finding two species of elegantly coloured true *Planaria* inhabiting the dewy forest ! The false relation they bear to snails is the most extraordinary thing of the kind I have ever seen.’¹

Many years later, in 1867, he wrote to Fritz Müller suggesting that the resemblance of a soberly coloured British Planarian to a slug might be due to Mimicry.²

The most interesting copy of Bates’s classical memoir on Mimicry,³ read before the Linnean Society in 1861, is that given by him to the man who has done most to support and extend the

¹ *More Letters*, i. 9.

² *Life and Letters*, iii. 71.

³ ‘Contributions to an Insect Fauna of the Amazon Valley,’ *Trans. Linn. Soc.*, xxiii. 1862, 495

theory. My kind friend has given that copy to me; it bears the inscription:—

*Mr A. R. Wallace from his
do travelling companion the Author*

Only a year and a half after the publication of the *Origin*, we find that Darwin wrote to Bates on the subject which was to provide such striking evidence of the truth of Natural Selection:—

‘I am glad to hear that you have specially attended to “mimetic” analogies—a most curious subject: I hope you publish on it. I have for a long time wished to know whether what Dr. Collingwood asserts is true—that the most striking cases generally occur between insects inhabiting the same country.’¹

The next letter, written about six months later, reveals the remarkable fact that the illustrious naturalist who had anticipated Edward Forbes in the explanation of arctic forms on alpine heights,² had also anticipated H. W. Bates in the theory of Mimicry:—

‘What a capital paper yours will be on mimetic re-

¹ The letter is dated April 4, 1861. *More Letters*, i. 183.

² ‘I was forestalled in only one important point, which my vanity has always made me regret, namely, the explanation by means of the Glacial period of the presence of the same species of plants and of some few animals on distant mountain summits and in the arctic regions. This view pleased me so much that I wrote it out in extenso, and I believe that it was read by Hooker some years before E. Forbes published his celebrated memoir on the subject. In the very few points in which we differed, I still think that I was in the right. I have never, of course, alluded in print to my having independently worked out this view.’ *Autobiography in Life and Letters*, i. 88

semblances ! You will make quite a new subject of it. I had thought of such cases as a difficulty ; and once, when corresponding with Dr. Collingwood, I thought of your explanation ; but I drove it from my mind, for I felt that I had not knowledge to judge one way or the other. Dr. C., I think, states that the mimetic forms inhabit the same country, but I did not know whether to believe him. What wonderful cases yours seem to be !'¹

The above passage will probably be as great a surprise to other naturalists as it was to the present writer. It would be very interesting to know whether Collingwood published any statements on the subject. His book,² quoted by Darwin in the *Descent of Man*, is dated 1868.

Bates read his paper before the Linnean Society, Nov. 21, 1861, and Darwin's impressions on hearing it were conveyed in a letter to the author dated Dec. 3 :—

'Under a general point of view, I am quite convinced (Hooker and Huxley took the same view some months ago) that a philosophic view of nature can solely be driven into naturalists by treating special subjects as you have done. Under a special point of view, I think you have solved one of the most perplexing problems which could be given to solve.'³

The memoir appeared in the following year, and after reading it Darwin wrote as follows, Nov. 20, 1862 :—

'... In my opinion it is one of the most remarkable and admirable papers I ever read in my life. . . . I am rejoiced

¹ The letter is dated Sept. 25, 1861. *More Letters*, i. 197.

² C. Collingwood, *Rambles of a Naturalist on the shores and waters of the China Seas*, London, 1868.

³ *Life and Letters*, ii. 378

that I passed over the whole subject in the *Origin*, for I should have made a precious mess of it. You have most clearly stated and solved a wonderful problem. . . . Your paper is too good to be largely appreciated by the mob of naturalists without souls ; but, rely on it, that it will have *lasting* value, and I cordially congratulate you on your first great work. You will find, I should think, that Wallace will fully appreciate it.'¹

Four days later, Nov. 24, Darwin wrote to Hooker on the same subject :—

'I have now finished this paper . . . ; it seems to me admirable. To my mind the act of segregation of varieties into species was never so plainly brought forward, and there are heaps of capital miscellaneous observations.'²

Darwin was here referring to the tendency of similar varieties of the same species to pair together, and on Nov. 25 he wrote to Bates asking for fuller information on this subject.³ If Bates's opinion were well founded, Sexual Selection would bear a most important part in the establishment of such species.⁴ It must be admitted, however, that the evidence is as yet quite insufficient to establish this conclusion. It is interesting to observe how Darwin at once fixed on the part of Bates's memoir which seemed to bear upon Sexual Selection. A review of Bates's theory of Mimicry was contributed by Darwin to the *Natural History*

¹ *Life and Letters*, ii. 391-3.

² *More Letters*, i. 214.

³ *More Letters*, i. 215. See also parts of Darwin's letter to Bates in *Life and Letters*, ii. 392.

⁴ See Poulton, *Essays on Evolution*, 1908, 65, 85-8.

*Review*¹ and an account of it is to be found in the *Origin*² and in the *Descent of Man*.³

Darwin continually writes of the value of hypothesis as the inspiration of inquiry. We find an example in his letter to Bates, Nov. 22, 1860: 'I have an old belief that a good observer really means a good theorist, and I fully expect to find your observations most valuable.'⁴ Darwin's letter refers to many problems upon which Bates had theorized and observed, but as regards Mimicry itself, the hypothesis was thought out after his return home from the Amazons, when he no longer had the opportunity of testing it by the observation of living Nature. It is by no means improbable that, had he been able to apply this test, Bates would have recognized that his division of butterfly resemblances into two classes—one due to the theory of Mimicry, the other to the influence of local conditions—could not be sustained.

Fritz Muller's contributions to the problem of Mimicry were all made in S.E. Brazil, and numbers of them were communicated, with other observations on natural history, to Darwin, and by him sent to Professor R. Meldola who published many of the facts. Darwin's letters to Meldola⁵ contain abundant proofs of his interest in Müller's work upon Mimicry. One deeply

¹ New Ser., iii 1863, 219.

² Ed 1872, 375-8.

³ Ed. 1874, 323-5

⁴ *More Letters*, i. 176.

⁵ Poulton, *Charles Darwin and the theory of Natural Selection*, Lond. (1896), 199-218.

interesting letter¹ dated Jan. 23, 1872, proves that Fritz Müller before he originated the theory of Common Warning Colours (Synaposematic Resemblance or Müllerian Mimicry), which will ever be associated with his name, had conceived the idea of the production of mimetic likeness by Sexual Selection.

Darwin's letter to Meldola shows that he was by no means inclined to dismiss the suggestion as worthless, although he considered it daring.

'You will also see in this letter a strange speculation, which I should not dare to publish, about the appreciation of certain colours being developed in those species which frequently behold other forms similarly ornamented. I do not feel at all sure that this view is as incredible as it may at first appear. Similar ideas have passed through my mind when considering the dull colours of all the organisms which inhabit dull-coloured regions, such as Patagonia and the Galapagos Is.'²

A little later, on April 5, he wrote to Professor August Weismann on the same subject:—

'It may be suspected that even the habit of viewing differently coloured surrounding objects would influence their taste, and Fritz Müller even goes so far as to believe that the sight of gaudy butterflies might influence the taste of distinct species.'³

This remarkable suggestion affords interesting evidence that F. Müller was not satisfied with the sufficiency of Bates's theory. Nor is this surprising when we think of the numbers of

¹ Ibid., 201, 202.

² Darwin wrote, Aug. 2, 1871, in very similar terms to Fritz Müller himself. *Life and Letters*, iii. 151. ³ *Life and Letters*, iii. 157.

abundant conspicuous butterflies which he saw exhibiting mimetic likenesses. The common instances in his locality, and indeed everywhere in tropical America, were anything but the hard-pressed struggling forms assumed by the theory of Bates. They belonged to the groups which were themselves mimicked by other butterflies. Fritz Müller's suggestion also shows that he did not accept Bates's alternative explanation of a superficial likeness between models themselves, based on some unknown influence of local physico-chemical forces. At the same time Müller's own suggestion was subject to this apparently fatal objection, that the Sexual Selection he invoked would tend to produce resemblances in the males rather than the females, while it is well known that when the sexes differ the females are almost invariably more perfectly mimetic than the males and in a high proportion of cases are mimetic while the males are non-mimetic.

The difficulty was met several years later by Fritz Müller's well-known theory, published in 1879,¹ and immediately translated by Meldola and brought before the Entomological Society.² Darwin's letter to Meldola dated June 6, 1879, shows 'that the first introduction of this new and most suggestive hypothesis into this country was due to the direct influence of Darwin himself, who brought it before the notice of the one man who was likely to appreciate it at its true value

¹ *Kosmos*, May, 1879, 100.

² *Proc. Ent. Soc. Lond.*, 1879, xx.

and to find the means for its presentation to English naturalists.'¹ Of the hypothesis itself Darwin wrote, 'F. Müller's view of the mutual protection was quite new to me.'² The hypothesis of Müllerian Mimicry was at first strongly opposed. Bates himself could never make up his mind to accept it. As the Fellows were walking out of the meeting at which Professor Meldola explained the hypothesis, an eminent entomologist, now deceased, was heard to say to Bates: 'It's a case of save me from my friends!' The new ideas encountered and still encounter to a great extent the difficulty that the theory of Bates had so completely penetrated the literature of natural history. The present writer has observed that naturalists who have not thoroughly absorbed the older hypothesis are usually far more impressed by the newer one than are those whose allegiance has already been rendered. The acceptance of Natural Selection itself was at first hindered by similar causes, as Darwin clearly recognized:—

'If you argue about the non-acceptance of Natural Selection, it seems to me a very striking fact that the Newtonian theory of gravitation, which seems to every one now so certain and plain, was rejected by a man so extraordinarily able as Leibnitz. The truth will not penetrate a preoccupied mind.'³

¹ *Charles Darwin and the theory of Natural Selection*, 214.

² *Ibid.*, 213.

³ To Sir J. Hooker, July 28, 1868, *More Letters*, i. 305. See also the letter to A. R. Wallace, April 30, 1868, in *More Letters*, ii. 77, lines 6-8 from top.

There are many naturalists, especially students of insects, who appear to entertain an inveterate hostility to any theory of Mimicry. Some of them are eager investigators in the fascinating field of geographical distribution, so essential for the study of Mimicry itself. The changes of pattern undergone by a species of *Erebia* as we follow it over different parts of the mountain ranges of Europe is indeed a most interesting inquiry, but not more so than the differences between e.g. the *Acraea johnstoni* of S.E. Rhodesia and of Kilimanjaro. A naturalist who is interested by the *Erebia* should be equally interested by the *Acraea*; and so he would be if the student of Mimicry did not also record that the characteristics which distinguish the northern from the southern individuals of the African species correspond with the presence, in the north but not in the south, of certain entirely different butterflies. That this additional information should so greatly weaken, in certain minds, the appeal of a favourite study, is a psychological problem of no little interest. This curious antagonism is I believe confined to a few students of insects. Those naturalists who, standing rather farther off, are able to see the bearings of the subject more clearly, will usually admit the general support yielded by an ever-growing mass of observations to the theories of Mimicry propounded by H. W. Bates and Fritz Muller. In like manner Natural Selection itself was in the early days

often best understood and most readily accepted by those who were not naturalists. Thus Darwin wrote to D. T. Ansted, Oct. 27, 1860 :—

‘I am often in despair in making the generality of *naturalists* even comprehend me. Intelligent men who are not naturalists and have not a bigoted idea of the term species, show more clearness of mind.’¹

Even before the *Origin* appeared Darwin anticipated the first results upon the mind of naturalists. He wrote to Asa Gray, Dec. 21, 1859 :—

‘I have made up my mind to be well abused ; but I think it of importance that my notions should be read by intelligent men, accustomed to scientific argument, though *not* naturalists. It may seem absurd, but I think such men will drag after them those naturalists who have too firmly fixed in their heads that a species is an entity.’²

Mimicry was not only one of the first great departments of zoological knowledge to be studied under the inspiration of Natural Selection, it is still and will always remain one of the most interesting and important of subjects in relation to this theory as well as to evolution. In Mimicry we investigate the effect of environment in its simplest form : we trace the effects of the pattern of a single species upon that of another far removed from it in the scale of classification. When there is reason to believe that the model is an invader from another region and has only recently become an element in the environment

¹ *More Letters*, i. 175.

² *Life and Letters*, ii. 245. See also pp. 32-3 of the present work.

of the species native to its second home, the problem gains a special interest and fascination.¹ We are chiefly dealing with the fleeting and changeable element of colour, and we expect to find and we do find evidence of a comparatively rapid evolution. The invasion of a fresh model is for certain species an unusually sudden change in the forces of the environment, and in some instances we have grounds for the belief that the mimetic response has not been long delayed.

MIMICRY AND SEX

Ever since Wallace's classical memoir on Mimicry in the Malayan swallow-tail butterflies, those naturalists who have written on the subject have followed his interpretation of the marked prevalence of mimetic resemblance in the female sex as compared with the male. They have believed with Wallace that the greater dangers of the female, with slower flight and often alighting for oviposition, have been in part met by the high development of this special mode of protection. The fact cannot be doubted. It is extremely common for a non-mimetic male to be accompanied by a beautifully mimetic female and often by two or three different forms of female, each mimicking a different model. Indeed in these latter cases the male is usually non-mimetic (e. g. *Papilio dardanus* = *merope*), or if a mimic

¹ See pp. 159-77, which are devoted to the detailed consideration of an example of this kind.

(e. g. the Nymphaline genus *Euripus*) resembles a very different model. On the other hand, a non-mimetic female accompanied by a mimetic male is excessively rare. An example is afforded by the Oriental Nymphaline, *Cethosia*, in which the males of some species are rough mimics of the brown Danaines. When both sexes mimic, it is very common for the females to be better and often far better mimics than the males.

Predominant female Mimicry is characteristic of butterflies and very rare in moths. If examples occur at all among the numberless mimetic Diptera, Coleoptera, &c., they are probably excessively scarce. In some of the orb-weaving spiders, however, the males mimic ants, while the much larger females are non-mimetic.

Although still believing that Wallace's hypothesis in large part accounts for the facts briefly summarized above, the present writer has recently been led to doubt whether it offers a complete explanation. Mimicry in the male, even though less beneficial to the species than Mimicry in the female, would still surely be advantageous. Why then is it so often entirely restricted to the female? While the attempt to find an answer to this question was haunting me, I re-read a letter written by Darwin to Wallace, April 15, 1868, containing the following sentences :—

‘When female butterflies are more brilliant than their males you believe that they have in most cases, or in all

cases, been rendered brilliant so as to mimic some other species, and thus escape danger. But can you account for the males not having been rendered equally brilliant and equally protected? Although it may be most for the welfare of the species that the female should be protected, yet it would be some advantage, certainly no disadvantage, for the unfortunate male to enjoy an equal immunity from danger. For my part, I should say that the female alone had happened to vary in the right manner, and that the beneficial variations had been transmitted to the same sex alone. Believing in this I can see no improbability (but from analogy of domestic animals a strong probability) that variations leading to beauty must often have occurred in the males alone, and been transmitted to that sex alone. Thus I should account in many cases for the greater beauty of the male over the female, without the need of the protective principle.¹

The consideration of the facts of Mimicry thus led Darwin to the conclusion that the female happens to vary in the right manner more commonly than the male, while the secondary sexual characters of males supported the conviction 'that from some unknown cause such characters [viz. new characters arising in one sex and transmitted to it alone] apparently appear oftener in the male than in the female'.²

Comparing these conflicting arguments, we are

¹ *More Letters*, ii. 73, 74 On the same subject—'the gay-coloured females of *Pieris*' (*Perrhybris* (*Mylothris*) *pyrrha* of Brazil), Darwin wrote to Wallace, May 5, 1868, as follows: 'I believe I quite follow you in believing that the colours are wholly due to mimicry; and I further believe that the male is not brilliant from not having received through inheritance colour from the female, and from not himself having varied, in short, that he has not been influenced by selection.' It should be noted that the male of this species does exhibit a mimetic pattern on the under surface.—*More Letters*, ii. 78.

² Letter from Darwin to Wallace, May 5, 1867, *More Letters*, ii. 61.

led to believe that the first is the stronger. Mimicry in the male would be no disadvantage but an advantage, and when it appears would be and is taken advantage of by selection. The secondary sexual characters of males would be no advantage but a disadvantage to females, and, as Wallace thinks, are withheld from this sex by selection. It is indeed possible that Mimicry has been hindered and often prevented from passing to the males by Sexual Selection. We know that Darwin was much impressed¹ by Thomas Belt's daring and brilliant suggestion that the white patches which exist, although ordinarily concealed, on the wings of mimetic males of certain *Pierinae* (*Dismorphia*), have been preserved by preferential mating. He supposed this result to have been brought about by the females exhibiting a deep-seated preference for males that displayed the chief ancestral colour, inherited from periods before any mimetic pattern had been evolved in the species. But it has always appeared to me that Belt's deeply interesting suggestion requires much solid evidence and repeated confirmation before it can be accepted as a valid interpretation of the facts.

In the present state of our knowledge, at any rate of insects and especially of Lepidoptera, it is probable that the female is more apt to vary than the male, and that an important element in the interpretation of prevalent female Mimicry is provided

¹ *Descent of Man*, 325.

by this fact. In order adequately to discuss the question of Mimicry and sex it would be necessary to analyse the whole of the facts, so far as they are known in butterflies. On the present occasion it is only possible to state the inferences which have been drawn from general impressions—inferences which it is believed will be sustained by future detailed inquiry.

(1) Mimicry may occasionally arise in one sex because the differences which distinguish it from the other sex happen to be such as to afford a starting-point for the resemblance. Here the male is at no disadvantage as compared with the female, and the rarity of Mimicry in the male alone (e.g. *Cethosia*) is evidence that the great predominance of female Mimicry is not to be thus explained.

(2) The greater colour-variability of the female, observed at least in certain groups of butterflies, and especially her more pronounced tendency to dimorphism and polymorphism, have been of much importance in determining this predominance. Thus if the female appear in two different forms and the male in only one, it will be twice as probable that she will happen to possess a sufficient foundation for the evolution of Mimicry.

(3) The appearance of melanic or partially melanic forms in the female has been of very great service, providing as it does a change of ground-colour. Thus the Mimicry of the black

generally red-marked American 'Aristolochia swallow-tails' (*Pharmacophagus*) by the females of *Papilio* swallow-tails was probably begun in this way.

(4) It is probably incorrect to assume with Haase that Mimicry always arose in the female and was later acquired by the male. Both sexes of the third section of swallow-tails (*Cosmodesmus*) mimic *Pharmacophagus* in America, far more perfectly than do the females of *Papilio*. But this is not due to *Cosmodesmus* presenting us with a later stage of the history begun in *Papilio*; for in Africa *Cosmodesmus* is still mimetic (of *Danainae*) in both sexes although the resemblances attained are imperfect, while many African species of *Papilio* have non-mimetic males with beautifully mimetic females. The explanation is probably to be sought in the fact that the females of *Papilio* are more variable and more often tend to become dimorphic than those of *Cosmodesmus*, while the latter group has more often happened to possess a sufficient foundation for the origin of the resemblance, in patterns which, from the start, were common to male and female.

(5) In very variable species with sexes alike, Mimicry can be rapidly evolved in both sexes out of very small beginnings. Thus the reddish marks which are common in many individuals of *Limenitis arthemis* were almost certainly the starting-point for the evolution of the beautifully mimetic *L. archippus*. Nevertheless in such

cases, although there is no reason to suspect any greater variability, the female is commonly a somewhat better mimic than the male and often a very much better mimic. Wallace's principle seems here to supply the obvious interpretation ; but it is to be noted that the evolution of Mimicry is taking place in colours that are associated with sex. Otherwise, it is impossible to explain the fact that the more perfect Mimicry attained by one sex is not immediately transferred to the other.

(6) When the difference between the patterns of model and presumed ancestor of mimic is very great, the female is often alone mimetic ; when the difference is comparatively small, both sexes are commonly mimetic. The Nymphaline genus *Hypolimnas* is a good example. In *Hypolimnas* itself the females mimic *Danainae* with patterns very different from those preserved by the non-mimetic males : in the sub-genus *Euralia*, both sexes resemble the black and white Ethiopian Danaines with patterns not very dissimilar from that which we infer to have existed in the non-mimetic ancestor.

(7) Although a melanic form or other large variation may be of the utmost importance in facilitating the start of a mimetic likeness, it is impossible to explain the evolution of any detailed resemblance in this manner. And even the large colour variation itself may well be the expression of a minute and 'continuous' change

in the chemical and physical constitution of pigments.

(8) Female Mimicry is not by any means always a question of colour and pattern alone. Thus, the mimetic females of some *Papilionidae* lose the 'tails' which are retained by the non-mimetic males (e. g. *P. dardanus* = *merope*), and the females of the tropical American Nymphaline genus *Eresia* and Pierine genus *Dismorphia* and its allies, are not only better mimics in colour and pattern but also in shape of the wings.

SEXUAL SELECTION (EPIGAMIC CHARACTERS)

We do not know the date at which the idea of Sexual Selection arose in Darwin's mind, but it was probably not many years after the 'sudden flash of insight' which, in October, 1838, gave to him the theory of Natural Selection. An excellent account of Sexual Selection occupies the concluding paragraph of Part I of Darwin's Section of the Joint Essay on Natural Selection, read July 1, 1858, before the Linnean Society.¹ The principles are so clearly and sufficiently stated in these brief sentences that it is appropriate to quote the whole :

'Besides this natural means of selection, by which those individuals are preserved, whether in their egg, or larval, or mature state, which are best adapted to the place they fill in nature, there is a second agency at work in most unisexual animals, tending to produce the same effect, namely, the struggle of the males for the females. These struggles are

¹ *Journ. Proc. Linn. Soc.*, iii. 1859, 50.

generally decided by the law of battle, but in the case of birds, apparently, by the charms of their song, by their beauty or their power of courtship, as in the dancing rock-thrush of Guiana. The most vigorous and healthy males, implying perfect adaptation, must generally gain the victory in their contests. This kind of selection, however, is less rigorous than the other; it does not require the death of the less successful, but gives to them fewer descendants. The struggle falls, moreover, at a time of year when food is generally abundant, and perhaps the effect chiefly produced would be the modification of the secondary sexual characters, which are not related to the power of obtaining food, or to defence from enemies, but to fighting with or rivalling other males. The result of this struggle amongst the males may be compared in some respects to that produced by those agriculturists who pay less attention to the careful selection of all their young animals, and more to the occasional use of a choice mate.'

A full exposition of Sexual Selection appeared in the *Descent of Man* in 1871, and in the greatly augmented second edition, in 1874. It has been remarked that the two subjects, *The Descent of Man* and *Selection in Relation to Sex*, seem to fuse somewhat imperfectly into the single work of which they form the title. The reason for their association is clearly shown in a letter to Wallace, dated May 28, 1864: '... I suspect that a sort of sexual selection has been the most powerful means of changing the races of man.'¹

Darwin, as we know from his Autobiography,² was always greatly interested in this hypothesis, and it has been shown in the preceding pages that he was inclined to look favourably upon it

¹ *More Letters*, ii. 33.

² *Life and Letters*, i. 94.

as an interpretation of many appearances usually explained by Natural Selection. Hence Sexual Selection, incidentally discussed in other sections of the present essay, need not be considered at any length, in the section specially allotted to it.

Although so interested in the subject and notwithstanding his conviction that the hypothesis was sound, Darwin was quite aware that it was probably the most vulnerable part of the *Origin*. Thus he wrote to H. W. Bates, April 4, 1861 :—

‘If I had to cut up myself in a review I would have [worried?] and quizzed sexual selection; therefore, though I am fully convinced that it is largely true, you may imagine how pleased I am at what you say on your belief.’¹

The existence of sound-producing organs in the males of insects was, Darwin considered, the strongest evidence in favour of the operation of Sexual Selection in this group.² Such a conclusion has received strong support in recent years by the numerous careful observations of Dr. F. A. Dixey³ and Dr. G. B. Longstaff⁴ on the scents of male butterflies. The experience of these naturalists abundantly confirms and extends the account given by Fritz Müller⁵ of the scents of certain Brazilian butterflies. It is a remarkable fact that the apparently epigamic scents of male butterflies should be pleasing to

¹ *More Letters*, i. 183.

² *Life and Letters*, iii. 94, 138.

³ *Proc. Ent. Soc. Lond.*, 1904, lvi.; 1905, xxxvii., liv.; 1906, ii.

⁴ *Proc. Ent. Soc. Lond.*, 1905, xxlv., *Trans. Ent. Soc. Lond.*, 1905, 136; 1908, 607.

⁵ *Jen. Zeit.*, xi., 1877, 99; *Trans. Ent. Soc. Lond.*, 1878, 211.

man while the apparently aposematic scents in both sexes of species with warning colours should be displeasing to him. But the former is far more surprising than the latter. It is not perhaps astonishing that a scent which is *ex hypothesi* unpleasant to an insect-eating Vertebrate should be displeasing to the human sense; but it is certainly wonderful that an odour which is *ex hypothesi* agreeable to a female butterfly should also be agreeable to man.

Entirely new light upon the seasonal appearance of epigamic characters is shed by the recent researches of C. W. Beebe,¹ who caused the scarlet tanager (*Piranga erythromelas*) and the bobolink (*Dolichonyx oryzivorus*) to retain their breeding plumage through the whole year by means of fattening food, dim illumination and reduced activity. Gradual restoration to the light and the addition of meal-worms to the diet invariably brought back the spring song, even in the middle of winter. A sudden alteration of temperature, either higher or lower, caused the birds nearly to stop feeding, and one tanager lost weight rapidly and in two weeks moulted into the olive-green winter plumage. After a year, and at the beginning of the normal breeding season, 'individual tanagers and bobolinks were gradually brought under normal conditions and activities,' and in every case moulted from nuptial plumage to nuptial plumage. 'The dull colors of

¹ *The American Naturalist*, xlu. No. 493, Jan. 1908, 34.

the winter season had been skipped.' The author justly claims to have established 'that the sequence of plumage in these birds is not in any way predestined through inheritance. . . . , but that it may be interrupted by certain factors in the environmental complex'.

Mr. Beebe's deeply interesting investigations on birds prove that external stimulus may be as necessary for the production of the tints displayed in courtship as for other colours that are characteristic of the species (p. 110). Birds may thus exhibit the individual susceptibility to environment so well known in numbers of insect larvae and pupae (p. 109). Although certain naturalists, especially the students of plant oecology,¹ consider that results of this kind are opposed to a Darwinian interpretation, it is perfectly clear that 'the changes so produced must, like any other variations, pass through the ordeal of the survival of the fittest'.² And when each possible response is appropriate to the special environment which provides the stimulus, it is obvious that, so far from witnessing the elimination of Natural Selection, we are in presence of its highest manifestation.

¹ See J. M. Coulter in *Fifty Years of Darwinism*, New York, 1909, 61-3.

² Editors of *More Letters*, i. 214 n. 1.

VI

MIMICRY IN THE BUTTERFLIES OF NORTH AMERICA

Written from the notes of the Anniversary Address delivered to the Entomological Society of America, Baltimore, Thursday, December 31, 1908.

INTRODUCTORY

WITHIN a few weeks of the hundredth anniversary of Darwin's birth, and nearly midway between the fiftieth anniversaries of the publication of Natural Selection on July 1 last and the *Origin of Species* on Nov. 24 next, it seemed to me specially appropriate to select for this address a subject that is closely associated with Darwinian teachings. Although he did not publish it during his lifetime, we now know from his correspondence that Darwin independently originated the interpretation of Mimicry which was afterwards suggested by H. W. Bates.¹ Its development in the mind of the naturalist of the Amazons and the rival theory afterwards suggested by Fritz Müller, were both of them the direct outcome, in Bates's case the very speedy outcome, of the *Origin*. The deep interest which Darwin took in the

hypotheses of both naturalists is proved by many a letter in his published correspondence.¹ All this forms a peculiarly fascinating chapter of ancient history,—nevertheless ancient history; but if we desire to choose a subject because of the light it can throw to-day and is certain to throw to-morrow upon evolution and its causes, there is no study which for promise as well as performance can be set on a higher level than Mimicry.

In the course of the following address the word ‘Mimicry’ will be used with the restricted meaning attached to it by A. R. Wallace. It will be applied solely to the superficial resemblances between animals, and not to their likeness to vegetable or mineral surroundings for the purpose of concealment.

The study of Mimicry is of the highest value in relation to both evolution itself and the motive causes of evolution.

Apart from all question of the means by which Mimicry has been produced, it will be generally admitted that the mimetic species has in some way evolved a superficial resemblance to the pattern of one or more species, more or less remote from it in the scale of classification. Looking on the changes by which the resemblance has been produced as a piece of evolutionary history, and, as I have said, disregarding for the moment their causes, we have one of the

¹ See pp. 123-9.

very simplest and sharpest pictures of organic transformation presented for our investigation. An effect—generally a strongly marked and conspicuous effect—has been brought about in those elements which make up the superficial appearance of a species, and this important change is manifestly in the direction of only a minute fraction of the infinitely complex organic environment, viz. that fraction contributed by the superficial appearance of one or more very different species, commonly indeed of but a single one. When, as in North America, a recent invader becomes the model determining the direction of evolution in some constituent of the ancient butterfly fauna, the case becomes especially striking.

The effects produced on the mimic are generally sharper and more distinct than those seen in the concealing resemblances to bark, lichen, earth, &c.,—the difference corresponding to the more definite and individual appearance usually presented by the pattern of the model as compared with such elements in the vegetable and mineral surroundings. There are also other important differences. The models of Mimicry are generally more restricted in their range, and differ more widely in different areas and in different parts of the same area than the models of cryptic resemblance. Differences between the local forms of the same model imply that the mimicked species has itself been subject to rapid

change, while the models of cryptic resemblance appear by comparison to be stereotyped and permanent. Furthermore the models as well as their mimics within the same area are liable to changes of distribution, whereas the models of cryptic resemblance are as a rule comparatively fixed. A mimetic species may often be found passing into an area where its model exists in a different form or does not exist at all, and highly instructive conclusions may be drawn from the study of the corresponding changes.

In accordance with the facts briefly summarized in the above statements, we find that better and more numerous examples of rapid recent change are to be found in mimetic patterns than in those which promote concealment. Not only is this evident when we trace the geographical changes of model and mimic over a wide continuous area, but in many cases the same genus includes both mimetic and non-mimetic species, the latter enabling us to infer with more or less certainty the ancestral appearance of the former. The history thus unravelled may often be further confirmed by a study of the non-mimetic males of mimetic females.

Many naturalists at the present day incline to return to the old belief that the history of evolution has been 'discontinuous', proceeding by 'mutations' or large and definite steps of change. The comprehensive and detailed study of Mimicry as a piece of biological history certainly provides

one of the best and safest means—perhaps the very best—of forming a judgement between this revived opinion and Darwin's conclusion that, although the rate of transformation varied greatly and might slow down to nothing for long periods, the steps of change were small, forming a gradual and 'continuous' transition between the successive forms in the same evolutionary history.¹

The study of the causes of Mimicry is more difficult than that of the history of Mimicry, the conclusions far less certain. Nevertheless the evidence at present available yields much support to the theory of Natural Selection as the motive cause of evolution. The facts certainly do not point to any other interpretation. They negative the conclusion that mimetic resemblances have been produced by the direct action of external forces (Hypothesis of External Causes) or by variation unguided by selection (Hypothesis of Internal Causes). Nor do they support Fritz Müller's earlier and daring speculation (see pp. 127-8) that female preferences were influenced by the sight of the patterns displayed by the models (Hypothesis of Sexual Selection). The only hypotheses which are in any way consistent with the body of facts, considered as a whole, are those which assume that the resemblances in question have been built up by the selection of variations beneficial in the struggle for life.

In its concentration on a minute fraction of the

¹ See pp. 42-51, also Appendix B, p. 254.

total organism as well as in the rapidity of the results achieved, the operation of Natural Selection in the production of Mimicry is more than ordinarily akin to the methods of Artificial Selection. Indeed a very fascinating and promising line of investigation in a suitable locality would be the attempt to initiate or improve a mimetic likeness by means of Artificial Selection.

Mimetic resemblances are of two kinds, respectively interpreted by two well-known hypotheses, both based on the theory of Natural Selection.

1. Mimicry as interpreted by H. W. Bates is an advantageous deceptive resemblance borne by palatable or harmless species (the mimics) to others that are unpalatable or otherwise specially defended (the models). Such resemblance will be spoken of as Batesian Mimicry, the examples as Batesian mimics, the interpretation as the Batesian Hypothesis.

2. The resemblances between specially defended species themselves, although well known to Bates, were not explained by his hypothesis as he conceived it. He suggested that they were an expression of the common results produced by forces common to the environment of the species in question. Such likenesses¹ were subsequently interpreted by Fritz Müller as the advantageous adoption of a common advertisement by specially

¹ It is probable that these were the examples which Fritz Müller had previously sought to explain by the theory of Sexual Selection. See pp. 127-8 of the present volume.

defended species, whereby the loss of life incurred during the education of young inexperienced enemies was contributed between the similar forms, instead of by each species independently as would have been the case if they had been dissimilar, and possessed patterns requiring each a separate education. Such resemblance will be spoken of as Müllerian Mimicry, the examples as Müllerian mimics, the interpretation as the Müllerian Hypothesis.

SPECIAL ADVANTAGES OF THE NORTH
AMERICAN BUTTERFLY FAUNA FOR
THE STUDY OF MIMICRY

The butterfly fauna of North America affords probably the best field in which to begin the study of Mimicry,—a subject which has been shown to possess the most profound significance in relation to the deepest problems by which the naturalist is confronted. The examples are sharp and striking, but not too numerous, and the inquiry can be approached without the confusion and excessive strain on the memory which must inevitably at first beset the student of Mimicry in the tropics. But outside the tropics it is also the best field for this study, as will be shown below.

The western section of the Palaearctic Region is sharply cut off by the Sahara from the Ethiopian, and its few examples of Mimicry are not such as would be likely to awaken the interest and enthusiasm of the beginner. The eastern Palaearctic

arctic section suffers from the opposite defect. Separated by imperfect barriers from the Oriental Region, its butterfly fauna is complicated by much invasion of specially protected species from the tropics, and the examples of Mimicry are too numerous and too little known. North America occupies a position conveniently intermediate between the two sections of the Palaearctic portion of the circumpolar land-belt. It has been invaded by models from the eastern tropics of the Old World and also probably from the tropics of the New; but the species are few and their effects upon the indigenous butterflies sharp and distinct. The Mimicry itself affords striking and remarkable evidence of the lines of migration followed by some of the intruding models. The ancestral forms from which the mimics were derived, have nearly always persisted, and enable us to unravel the history of the change, with exceptional clearness. The examples bear in a most interesting manner upon the two great hypotheses associated respectively with the names of H. W. Bates and Fritz Müller. Although the butterfly fauna is as well known as that of any part of the world, the mimetic resemblances supply material for a large amount of much-needed original investigation, inviting the attention of American naturalists in almost every locality.

THE DANAINAE MODELS OF NORTH AMERICA,
AND THEIR RELATIONSHIP TO THE SOUTH
AMERICAN AND OLD WORLD DANAINAE¹

The *Danainae* are the most important and most extensively mimicked of all specially protected butterflies in the Old World tropics. The *Acraeinae*, so abundant in Africa, are also greatly mimicked, but to a far less extent than the comparatively few species of *Danainae* found in the same Region,—all belonging to the section *Danaini*. The Ethiopian *Acraeas* in fact supply several mimics of the Danaines, but no example of the opposite relationship is known. In the tropical East, the *Acraeinae* are poorly represented, while the *Danainae* (*Danaini*, *Euploeini*, *Hestia*, *Hamadryas*) are dominant in numbers as well as in the power of influencing the patterns of other butterfly groups. In both Africa and the East, Mül-

¹ The subject of the address from this point onwards is treated in considerable detail in the author's memoir, *Mimetic North American species of the Genus Limenitis (s. l.) and their models*, in *Trans. Ent. Soc. Lond.*, 1908, 447-88. Dr. Jordan's later conclusions as to the affinities of *Danaida plexippus*, added to the memoir in a terminal note (488) and somewhat at variance with his earlier conclusions quoted in the text, are here adopted throughout. A broader and less detailed treatment is followed in this address, special attention being directed to the numerous points on which further observations are required. Where no other authority is mentioned I have followed the synonymy and geographical distribution of Scudder's great work, *Butterflies of the Eastern United States and Canada*, and, for the *Papilionidae*, Rothschild and Jordan's fine monograph (*Nov. Zool.*, xiii, 1906, 411-752). I have not, however, followed Scudder in the general use of *Basilarchia* as a generic name, because I think that the whole group of *Limenitis*, in its widest acceptation, requires revision, and that until this has been accomplished it is inexpedient to adopt the terminology proposed for a portion of it.

lerian Mimicry is evident between the different genera and sections of the specially protected groups themselves.

In the richest and most remarkable butterfly fauna in the world, that of South America, the dominant specially protected group is composed of the *Ithomiinae*, allied to the *Danainae*, and called by Bates 'Danaoid Heliconidae'. Next in importance come the *Heliconinae*, allied to the *Acraeinae*, and called by Bates 'Acraeoid Heliconidae'. Both of these are extensively mimicked, especially the *Ithomiinae*: in fact it was the close and obvious Mimicry of these by certain species of the *Heliconinae* that puzzled Bates and ultimately received an interpretation in the Müllerian Hypothesis. In addition to the above, this rich and varied Region contains numerous true *Acraeinae*, mimicked considerably, and a small number of true Danaine species. These latter, which are of extreme interest, fall into two groups. One of them, the *Lycoraeini*, containing the two genera *Lycorea* and *Ituna*, is confined to South America, and bears evident traces of long residence in the Region. The whole of the species are mimetic of various dominant Ithomiine genera, while at the same time some of them appear also to act as models for other butterflies, in a single case (*Ituna phenarete*) even for one of the rarer species (*Eutresis imitatrix*) belonging to the *Ithomiinae* themselves. It was the resemblance between the Lycoraeine genus *Ituna* and the Ithomiine

genus *Thyridia* that led Fritz Müller to his hypothesis, and formed the title of the paper in which he first expounded it. The *Lycoraeini* are widely different from any of the Old World *Danainae* and are sometimes separated from them as a distinct sub-family. The second group of Danaines, found in North America as well as South, belongs to the Old World section *Danaini*, and is in every respect strongly contrasted with the *Lycoraeini*. Its species, divided into two genera *Anosia* and *Tasitia* by Moore, are not known to enter into mimetic relations with any of the other butterflies of this southern Region.¹ Furthermore, they not only belong to a dominant Old World section of the Danaines, but are even closely allied to particular species within it. It is probable that there are only two well-marked species of *Danaini* on the American Continent, and that the various forms encountered over this vast area are the geographical races or sub-species of these two. In north temperate America they are the well-known models for mimicry,—*Anosia plexippus* extending far into Canada, and *Tasitia berenice* and its form *strigosa* not ranging beyond the southern States.

In 1897, at the Detroit meeting of the American Association for the Advancement of Science, I suggested ' that the Mimicry of *Anosia plexippus*

¹ It is possible, however, that there are incipient resemblances to *Anosia* in certain S. American *Acraeinae*

² *Proc. Am. Assoc. Adv. Sci.*, 1897, xlii. 244

by *Limenitis (Basilarchia) archippus* was evidence that the model had long resided in North America, and that we might on this ground alone, even if we had not abundant positive evidence of its gradually increasing spread in the Old World during the past half-century, infer that *Anosia* had reached Fiji, Australia, Hong-Kong, &c., in comparatively recent times. This conclusion can hardly be doubted, and the argument might have been extended to enable us to infer the ancestral line of migration by which North America itself had been reached by this form. But in 1897 I followed what appeared to be the general view, that, in the New World, the original stream of *Danaine* invasion had run from the American tropics northward,¹ nor did I observe that the evidence based on the growth of mimetic resemblance warranted the interesting conclusion that its flow had taken the opposite direction, and that the south had been peopled by way of the north. Accepting this conclusion the question arises: Whence came the *Danaini* of North America? The answer requires a somewhat careful comparison between the New and Old World butterflies of this group.

Among the commonest of the Old World *Danaini*, are certain species with tawny colouring, a black border, and black white-barred apex to the fore wing. The under surface is even more

¹ *Verhandl. d. V. Internat. Zool. Congr. z. Berlin*, 1901, Jena, 1902, 171. See also *Essays on Evolution* (1908), 274: also errata.

conspicuous than the upper, being brighter in colour and the black border marked with white in a more striking manner. In one set of Oriental species, placed by Moore in his genus *Salatura*, the veins are heavily marked with black on both surfaces, conferring a very characteristic appearance, especially upon the hind wing. The other set of species in which the veins are comparatively inconspicuous is placed by Moore in *Limnas*, including *L. chrysippus*, perhaps the commonest butterfly in the world, ranging from the Cape to Hong-Kong and perhaps to Japan. It is clear, however, that Africa is its ancestral home; for it is there mimicked far more extensively than in any other country.¹ In the Malay Archipelago, both *Salatura* and *Limnas* are represented by various forms, and in some of these the tawny colouring becomes much darkened. This tendency appears to be more frequent in *Limnas*, and when both forms have darkened in the same island (e g. Java) it is probable that *Limnas* has acted as the model for *Salatura*. There is a close general resemblance in colouring and pattern between *Salatura* of the Old World and *Anosia* of the New, as also between *Limnas* of the Old World and *Tasitia* of the New. Furthermore the two New World species differ from each other in the same points as do those of the Old. The dark, white-barred apex of the fore wing, so conspicuous in the Old World forms, is less

¹ *Proc. Am. Assoc. Adv. Sci.*, 1 c., 244

emphasized in those of the New, being especially evanescent in *Tasitia* where, however, traces of the white markings remain distinct. It is significant, however, that the black and white apex is also lost in one of the forms of *L. chrysippus*, viz. the variety *dorippus* (= *klugii*), abundant in many parts of Africa and also extending by way of Aden and the west coast of India as far as Ceylon. There is, in fact, much resemblance between the pattern of *dorippus* and such a form of *Tasitia* as *berenice*, the likeness being especially apparent in the indications of the former presence of the white apical bar. In the forms of *Tasitia*, as in some of *Limnas*, the ground-colour becomes darker and richer—a development especially well seen in *T. berenice* of Florida. Thus the two chief points in which the pattern of *Tasitia* differs from that of typical *L. chrysippus*, viz. the darker, richer ground-colour and the evanescent apical markings, are both presented by abundant Old World forms of the latter species. The superficial resemblances between these Old and New World Danaines are precise and often extend to minute details. Thus the scent-pouch on the hind wings of the male, best seen from the under surface, is similar in *Salatura* and *Anosia*, while the resemblance between *Limnas* and *Tasitia* in this respect is even more striking.

The resemblances above described suggested the investigation and comparison of structural characters in order still further to test the relationship

between these Old and New World Danaines, and also the validity of the genera created by Moore.¹ Such a comparison had already been partially made by Rothschild and Jordan, who in 1903 published the conclusion that *Limnas* and *Tasitia* cannot be generically separated.² I therefore wrote to my friend Dr. Jordan, asking if he would kindly extend his survey over all the four so-called genera. He found that in *Salatura genutia* and *Anosia plexippus*, having larvae with two pairs of filaments,³ the male genitalia are of the same type; while in *Limnas chrysippus* and *Tasitia berenice*, having larvae with three pairs of filaments, these genitalia are of a second type. The final opinion of this distinguished authority on the relationships between the Rhopalocera, was given in the following words⁴ :—

‘It appears to be certain that *Anosia plexippus* does not stand apart from the others. Therefore, if *Tasitia berenice*, *Limnas chrysippus* and *Salatura genutia* are placed in one

¹ *Proc. Zool. Soc. Lond.*, 1883, 201.

² *Not. Zool.* vol. x, Dec., 1903, 502.

³ Dr Jordan was at first inclined to think that *Anosia plexippus* should be separated generically, basing his conclusion in part on the larval characters (*Trans. Ent. Soc. Lond.*, 1908, 450). A more extended review of the Tring material pointed in the opposite direction, and Dr Jordan wrote on December 10, 1908, as follows:—
‘I find from our specimens [of preserved larvae] that—

(1) in *Euploea* (in the wide sense) there are 4 pairs of filaments, or three (the 3rd being absent), or two (the 3rd and 4th being absent).

(2) In *Danaidae*, incl. of *Anosia* & *Limnas*, there are 3 pairs (the 3rd of the 4 pairs of *Euploea* being absent), or 2 pairs (the 2nd and 3rd being absent). I find that, for instance, *genutia* and *purpurata* have 2 pairs only, like *plexippus*. The larva therefore does not furnish any argument for separating *plexippus* as a genus.’

⁴ In a letter to the author, dated December 15, 1908.

genus,¹ *plexippus* also must be included. I do not think you need hesitate thus to simplify the classification of these insects.'

I have no hesitation in accepting this advice, and in fusing all the four genera created by Moore into the single genus *Danaida*. Within this genus it has been made evident that the group of forms ranged around *Danaida plexippus* is the New World representative and close ally of the group of *D. genutia*; while that of *D. berenice* is similarly representative of the group of *D. chrysippus*. It is interesting to note that both the American Danaidas have become much larger than the corresponding Old World species, and that the most northern forms are larger than the southern in both hemispheres—the probable result of a slower metamorphosis in a more temperate climate.

EVIDENCE THAT DANAIDA IS AN OLD WORLD GENUS THAT HAS INVADED THE NEW

The suggestion might perhaps be made that the New World forms of *Danaida* are the more ancestral, and that those of the Old World have been derived from them by migration westward. There is no reason for concluding that the Danaidas of either geographical area possess a more primitive structure than those of the other; we are therefore driven to consult other lines of

¹ Dr. Jordan's opinion that these three genera should be united is quoted in *Trans. Ent. Soc. Lond.*, 1908, 450.

evidence. The following comparisons clearly indicate that *Danaida* is an Old World genus which has invaded America at no very remote period: (1) the far larger number of the Old World forms and the greater degree of specialization by which some of them are distinguished; (2) the place of *Danaida* as one out of a number of nearly related genera making up the *Danaini*, a large and dominant Old World group, *per contra* its isolated position in the New World; (3) The highly developed and complex mimetic relationships of the Old World *Danaidas*.

This last statement requires some expansion and exemplification. Allusion has already been made to the resemblances which have grown up between different species of *Danaida* in the same island,—resemblances in which the forms of *chrysippus* appear to act as models. Even more striking is the mimetic approach of certain Old World *Danaidas* to species of the other dominant Oriental section of the *Danainae*—the *Euploeini*. Thus in the Solomons, *Danaida* (*Salatura*) *insolata* is a beautiful mimic of the dark white-margined *Euploea brenchleyi*, while in the same islands, *Danaida* (*Salatura*) *decipiens* mimics the dark, white-spotted *Euploea asyllus*.¹ Finally, and most convincing as evidence of long residence, are the numbers of mimics which in the Old World have taken on the superficial appearance of species of

¹ See J. C. Moulton in *Trans. Ent. Soc. Lond.*, 1908, 603, 604: Pl. XXXIV, figs 5, 10.

Danaida. In addition to the extraordinary degree to which the Mimicry of *D. chrysippus* is carried in Africa, it is mimicked in the Oriental Region by the females of *Hypolimnas misippus* and of *Argynnis niphe*, and by the males of certain species of *Cethosia*. *Danaida genutia* and the forms related to it are also mimicked by male *Cethosias* and extensively by the females of species of *Elymninae*, while incipient Mimicry is seen in the males of some of them. With the exception of *Hypolimnas misippus*, common to both Regions, the Oriental mimics of *Danaida* do not approach the degree of resemblance attained by the best African mimics of *D. chrysippus*. It has already been pointed out that the Oriental mimics of this genus are far less numerous than the African. On the other hand, it is a curious fact that the only North American mimic of *D. plexippus*,—*Limenitis (Basilarchia) archippus*—reaches a far higher degree of resemblance than that attained by any of the characteristically Oriental mimics of *Danaida*.

The evidence as a whole enables us to decide that *Danaida* is an Old World genus and a comparatively recent intruder into America, while the perfection of the likeness attained by an indigenous American mimic proves that, under favourable circumstances, such resemblances may be rapidly produced. I do not, of course, mean to imply that the transformation was in any way sudden, or by other than minute transitional

steps. The evidence for this conclusion will be clearer when some of these steps have been described in detail (see pp. 164-8).

THE LINE OF MIGRATION BY WHICH DANAIDA ORIGINALLY ENTERED AMERICA

There can be little doubt that *D. plexippus* invaded America by way of the north, probably following the line of the Aleutian Islands. In North America it possesses an astonishing distribution for a member of so tropical a group, ranging immensely further north than any other Danaine in the world. Furthermore, *D. genutia*, the probable representative of its Old World ancestor, extends far beyond the tropics into Western and Central China. A study of the distribution of the Asclepiad food-plants on the eastern coast of Asia might perhaps throw light on the problem. *D. plexippus* was certainly the earlier of the two invaders of the New World. This is clearly shown by the extent of its own modification no less than by the changes it has itself produced. Its immense size, the shape of the hind-wing cell, and the form of the fore wings indicate that it is far more widely separated than is *D. berenice* from the nearest Old World species. It has furthermore been resident in North America long enough to effect profound changes in the pattern of an indigenous Nymphaline butterfly, rendering it an admirable mimic; whereas *D. berenice*, and probably its form *strigosa*

also, have only effected comparatively slight modifications in the mimetic pattern already produced under the influence of *plexippus* (see pp. 168-72). It is impossible to feel equal confidence in suggesting the line by which the later invasion of the more tropical *D. berenice* took place; but it is on the whole probable that it too came by way of the north during some temporary period of warmth. It is tolerably certain that it did not invade North America from the south. For although *D. berenice* and *strigosa* have produced—as is shown above—far less change in the indigenous N. American fauna than *plexippus*, they have still caused distinct and perfectly effective modifications in a single species; whereas in South America their representatives have not been shown to have had any effect at all. It is probable that both the American *Danaiidas* as they pressed southward were 'held up' for a considerable time at the northern borders of the Neotropical Region, unable at first to penetrate that crowded area. Finally they burst their way through and are now abundant throughout all the warmer parts of the Region, the forms of *plexippus* extending further into the temperate south, just as in the Northern Hemisphere they range further north than those of *berenice*. We are made to realize the recent date of the invasion of South America when we remember that nowhere else in the world do *Danaine* butterflies of equal abundance 'range

through a crowded area without producing any effect on any member of the Lepidopterous fauna, or without themselves being affected thereby.'¹ Abundant wide-ranging Danaines in the Old World, even when much smaller and with a less marked appearance, invariably produce some effect, and often themselves exhibit Müllerian resemblances.

THE EVOLUTION OF LIMENITIS (BASILARCHIA) ARCHIPPUS AS A MIMIC OF THE INVADING DANAIDA PLEXIPPUS

It has already been mentioned that a single species, undergoing corresponding modifications, provides a mimic for each of the three Danaïne models (including *strigosa*). We will first consider the well-known beautiful mimic of *D. plexippus*; for it undoubtedly arose earlier than the others.

The abundant *Limenitis* or *Basilarchia archippus* is closely related to the Palaearctic species of *Limenitis*, a group which includes the well-known British 'White Admiral' (*L. sylbella*). The example is unusually instructive, because the non-mimetic ancestor of the mimic is still very abundant in Canada and the north-eastern States, and we thus possess the material for reconstructing the history by which the one form originated from the other. We know that this ancestor, *Limenitis arthemis*, has persisted almost unchanged,

¹ *Trans Ent Soc Lond* (1908), 452

because of the resemblance between its pattern and that of other species of *Limenitis* (using the name in the broad sense) from all parts of the circumpolar land-belt, including North America itself. The difference between the pattern of the mimic and that of its non-mimetic parent is enormous—probably as great as that between any two butterflies in the world; but the steps by which the transition was effected were long ago suggested by S. H. Scudder,¹ and have recently been worked out in considerable detail by the present writer.²

L. arthemis exhibits the characteristic 'White Admiral' pattern—possessing on the upper surface a dark ground-colour with a broad white band crossing both wings, and white markings within the apex of the fore wing. Reddish or orange spots between the white bands and the margin are found in the hind wings of many individuals, more rarely in the fore wings. These latter markings are of the utmost importance, for, as Scudder long ago pointed out (l. c., 714), they undoubtedly provided the foundation for the change into the mimetic *archippus*.

A careful comparison between *arthemis* and *archippus* reveals the most conclusive evidence of selection. The one species has become changed into the other precisely as if an artist were to paint the pattern of *archippus* upon the wings

¹ *Butterflies of the Eastern United States and Canada*, Cambridge, Mass. (1889), 274, 714.

² *Trans. Ent. Soc. Lond.* (1908), 454-60

of *arthemis*, retaining unchanged every minute part of the old markings that could be worked into the new, and obliterating all the rest. Thus, extending in this direction and wiping out in that, the great transformation has been effected and one of the most beautiful mimics in the world produced.

The evolution of the mimetic pattern on the under surface has involved an even more elaborate change than on the upper; but it is not necessary to repeat here the details which have been only recently fully described.¹ I will, however, allude to the fate of the most conspicuous feature of *arthemis*, the broad white band crossing both wings. Save for the traces mentioned below, this marking has disappeared from both surfaces of the hind wing of *archippus*, but its black outer border is retained, and, cutting across the radiate pattern formed by the strongly blackened veins, detracts considerably from the mimetic resemblance.- On the under surface distinct

¹ *Trans. Ent. Soc. Lond.* (1908), 454-60.

² In the course of the address on December 31, 1908, I remarked that if we could revisit the earth in a few hundred years we might expect to find that this black line had disappeared from the hind wing, and the mimetic resemblance correspondingly heightened. At the conclusion, Mr. John H. Cook of Albany, N. Y., informed me that he had discovered near his home many individuals in which the black line was wanting from the upper surface. A few days later he very kindly sent me a record of his observations, of which an abstract is printed as a note at the end of this address (see pp. 211-12). The study of Mr. Cook's facts shows that near the city of Albany not only did the stripeless variety occur commonly (1 in 14), during the three seasons in which the observations were conducted, but also transitional forms with more or less broken stripes were far commoner than the normal *archippus* (18 to 1). The

traces of the white band may commonly be seen along the inner edge of the persistent black border. So far as my experience goes these traces are only to be found on the upper surface in the form *hulsti* (Edw.). The modification of the same marking in the fore wing is more interesting. Here towards the costal margin the black outer border is much expanded, invading the white band and cutting off from two to four white spots from its outer part. While the rest of the band disappears except on the costa itself, these black-surrounded white spots now represent the sub-apical pale-spotted black bar of the model. The new marking is larger and more conspicuous on the under surface, corresponding with the strong development of white on this surface of the model. The costal margin of the fore wing of the latter is streaked with long narrow white markings. In correspondence with this we find, commonly on the under surface, more rarely on the upper, that the extreme

fact that entirely stripeless individuals were invariably males is contrary to the rule that mimetic resemblance tends to develop more rapidly and fully in the other sex. But in this species I have observed another point in which the female tends to be more ancestral than the male, viz. the more frequent and complete development of the white spot in the cell of the fore-wing upper surface (a common feature of *Lamentis*, although now generally absent from *L. arthemis*).

Mr Cook's observations show that a single marking and one so simple that we might have expected it to act as a 'unit character', so small a fraction of the pattern that we could hardly speak of its sudden disappearance as 'discontinuous' evolution—that even this behaves differently on the two surfaces of the wing, while the individuals from which it has disappeared are immensely outnumbered by those in which it is transitional.

costal end of the white band is retained, often for the full breadth of the marking, forming a linear streak.

I have dwelt upon the changes undergone by the white band as an example of the way in which the new markings have been carved out of the old. The changes in the elaborate marginal pattern would have been equally convincing as evidence for a gradual and 'continuous' transformation.

THE MODIFICATION OF THE LIMENITIS MIMIC OF *DANAIDA PLEXIPPUS* INTO A MIMIC OF *D. BERENICE* IN FLORIDA

Danaida plexippus occurs together with *D. berenice* in Florida, but the latter far outnumber the former, and the modification of *Limenitis archippus* into the form *floridensis*, Strecker (= *eros*, Edw.) is probably entirely due to the predominance of one model over the other. Data for determining the exact proportions in various localities would be of high interest. There is no reason for believing that *berenice* is in any way more or less distasteful than *plexippus*, but its abundance makes it a more conspicuous feature in the environment.

It is evident that the change has been of the kind expressed in the above heading; for, as has been already implied on pp. 162-3, traces of the former Mimicry of *plexippus* persist in *floridensis* and tend to detract from the resemblance more

recently developed. This is especially the case with the conspicuously blackened veins of *archippus*, which are so important a feature in the likeness to *plexippus*. These, although obscured by the general darkening, are still recognizable in *floridensis*, diminishing its resemblance to *berenice* on the upper surface of both wings and on the under surface of the fore wing. Inasmuch as the details have been recently published elsewhere,¹ I will only dwell on one further point in the resemblance of *floridensis* to *berenice*—and that because the extensive observation of large numbers of specimens is greatly needed. I spoke on pp. 166-7 of the persistent traces of the white band on the hind-wing under surface in many individuals of *L. archippus*. These are ancestral features, diminishing the mimetic resemblance to *D. plexippus*. But in *D. berenice* there are conspicuous white spots towards the centre of the hind-wing under surface, and these, at any rate upon the wing, would bear some resemblance to the ancestral spots of the *Limentis* mimic. Now in my very limited experience of *floridensis* these spots were sometimes exceptionally developed and, outlined with black on their inner edges, were certainly far more distinct and conspicuous than in *L. archippus*. The appearances I witnessed suggested the possibility of the recall of a vanishing feature in consequence of

¹ *Trans Ent Soc Lond* (1908), 460, 461. See also Scudder, l. c., 718.

selection based on a likeness to certain white spots present in the new model (*berenice*) but absent from the old (*plerippus*). But many hundreds of specimens from different localities scattered over the total area of distribution require to be examined from this point of view. An even more interesting inquiry would be to trace the range of the *floridensis* form northward and determine the relationship of its limits to the zone in which *berenice* becomes scarce and disappears, and above all to ascertain whether *floridensis* on the borders of its range interbreeds with *archippus* and how far transitional varieties occur. Interbreeding between the two forms, if possible, would be of extraordinary interest. It is also of importance to ascertain precisely how far the one form penetrates the area of the other. Scudder indeed states that *floridensis* ranges into the Mississippi Valley and Dakota, far beyond the limits of *Danaula berenice*. It would be deeply interesting to make an exact comparison between such specimens and those from Florida, and also to ascertain the proportion which they bear to typical *archippus*. By far the most important feature in the evolution of *floridensis* is the general darkening of the ground-colour, and the material for such a transformation certainly exists freely in *archippus*, for the shade of brown varies immensely and may often be seen of as dark a tint as in *floridensis*, but not in my experience of precisely the same shade.

The proportion of such dark forms in various parts of the immense range of *archippus* would be another interesting inquiry.

THE MODIFICATION OF THE LIMENITIS MIMIC
OF DANAIDA PLEXIPPUS INTO A MIMIC OF
THE STRIGOSA FORM OF D. BERENICE IN
ARIZONA

The differences between *L. archippus* and the form *hulsti* (Edw.) are more striking than those which distinguish *floridensis* from the former. The upper surface of the hind wing of *hulsti* retains or more probably has recalled distinct traces of the white band, although the black stripe is evanescent. It is probable that, upon the wing, these vestigial white markings produce a general likeness to the pale-streaked hind-wing upper surface of *strigosa*. Other points in which *hulsti* differs from *archippus* and approaches *strigosa* are the reduction of black and the general appearance of the white spots in the subapical region of the fore wing, and the dull tint of the ground-colour. I have had hardly any experience of this interesting form and owe the above details to Dr. W. J. Holland's figure and description.¹ It is obvious that all the investigations suggested in the case of *floridensis* are, *mutatis mutandis*, equally available and equally important in the form *hulsti*.

¹ *Butterfly Book*, 84, 185, Pl. vii f. 5. Dr. Holland fully recognizes the mimetic significance of the pattern and colouring of *hulsti*.

The geographical distribution of *hulsti* strongly supports the conclusion that it was derived from *archippus* and not immediately from an *arthemis*-like ancestor. I have not yet had the opportunity of ascertaining whether this hypothesis is supported by evidence derived from a careful study of the pattern.

It is deeply interesting to observe that the same *Lamenitis arthemis*-like species, from which *archippus*, *floridensis* and *hulsti*—mimics respectively of the three *Danaidas*, *plexippus*, *berenice* and *strigosa*—have been directly or indirectly evolved, has also given rise to *L. astyanax (ursula)*, the mimic of a Papilionine model. Evidence in favour of the comparatively recent origin of these mimicking forms is to be found in the well-supported facts which indicate that *astyanax* still interbreeds with *arthemis* along their geographical overlap, and that it may even occasionally pair with the sister species *archippus*¹

The earlier stages of *archippus* and *astyanax* are, according to Scudder (l. c., 254, 255), with difficulty distinguished from those of *arthemis*, but *astyanax* presents the closer likeness of the two; a fact which, together with those referred to in the last paragraph, points to the conclusion that it arose even more recently than *archippus*.

The further consideration of *astyanax* is best deferred until some account has been given of the

¹ Scudder, l. c., 283, 289 *Trans. Ent. Soc. Lond.* (1908), 473, 474.

Papilionine models, and until certain general conclusions have been discussed in the following section.

BEARING UPON THEORIES OF MIMICRY OF
THE TRANSFORMATION WROUGHT BY THE
INVADING DANAIDAS

It has been shown that the Danaine models invaded America from the Old World tropics, probably following a northward route. Their patterns are but little changed in the new surroundings, and they still keep the characteristic appearance of Old World Danaidas. Furthermore, such changes as have taken place in the older invader, *D. plexippus*, during its residence in the New World, are also retained in those colonies which, during the past half-century, have been re-establishing themselves in the Old World. These facts support Darwin's conclusion that the physico-chemical influences of soil, climate, &c., are of comparatively slight importance, a conclusion which made him feel 'inclined to swear at the North Pole, and . . . to speak disrespectfully of the Equator'.

The mimics on the other hand are derived from characteristic and ancient inhabitants of the northern land-belt. If, as the followers of the theory of External Causes (see p. 148) maintain, species are the expression of the physical and

¹ In a letter to Sir Charles Lyell, Oct. 11, 1859 — *Life and Letters*, ii 212.

chemical forces of the environment, then the Danaïdas express the Old World tropics and the species of *Limenitis* the northern land-belt. We might expect on this theory that the Danaïdas, when they invaded the northern zone, might come to resemble the *Limenitis*; but the transformation that has actually occurred is entirely inconsistent with any such hypothesis. Although the Danaïdas have undergone no important change in the new environment, their presence has entirely transformed and brought into a close superficial resemblance to themselves the descendants of a member of an ancient group. Such a fact is inconsistent with any interpretation as yet offered except that which refers the change to the accumulation by selection of variations which promote a likeness to the Danaïdas.

The facts also bear upon the two theories of Mimicry associated with the names of H. W. Bates and Fritz Müller. According to Bates's theory, Mimicry is a special form of protective or cryptic resemblance. In the ordinary examples of this principle, species are aided in the struggle by concealment, by a likeness to some object of no interest to their enemies (such as bark, earth, &c.); in these special examples (called mimetic) species are aided by resembling some object which is unpleasant or even dangerous to their foes. Fritz Müller's theory of Mimicry includes the cases in which the mimics, as well as their models, are specially defended, although generally to an

unequal degree.¹ The resemblance is due to the advantages of a common advertisement. Before the growth of a mimetic likeness, Batesian mimics, it is reasonable to assume, belonged to the immense group of species possessing a cryptic appearance ; Mullerian mimics on the other hand may be assumed to have possessed warning or aposematic colours of their own previous to the adoption of those of another species. This test is more readily applied than might be supposed ; for a comparison with allied non-mimetic species, and with the non-mimetic males of mimetic females, will generally indicate whether the ancestral pattern of a species now mimetic belonged to the group of concealing colours or to that of warning.

The *Danaidas* invaded North America and entered an assemblage of butterflies of which the dominant species are ancient inhabitants of the northern land-belt. Among them are several, such as the species of *Grapta* or *Polygonia* (the 'Comma' butterflies), with beautifully cryptic patterns on the parts of the wing surface exposed in the resting position. No such forms have been influenced by the invaders, but with the whole fauna before them they have only produced changes in the dominant group *Limenitis*, known throughout the northern belt for a conspicuous under surface and a floating flight ; also believed to be mimicked by other butterflies, e.g. the females of the *Apaturas*

¹ It is probable that relative abundance may determine the relationship of model and mimic in cases where there is no reason for suspecting any difference in the degree of unpalatability.

('Purple Emperors') and the later brood of *Araschnia levana*.¹ Furthermore, the close allies of *Limnitis* in South America, the abundant *Adelphas*, are beautifully mimicked, not only by females of the genus *Chlorippe*, which represents *Apatura*, but also by *Erycinidae*. In another point the facts are at variance with Bates's interpretation but harmonize with Müller's. Bates supposed Mimicry to be an adaptation by which a scarce, hard-pressed form is enabled to hold its own in the struggle for existence. But *L. arthemis*, which represents with little or no change the species from which the mimics were derived, persists as a very abundant and flourishing species, while its mimetic descendant *archippus* has gained an immensely extended range and become almost universally commoner than any other species of its group (Scudder, l.c., 266). *L. archippus* extends from Hudson's Bay to the Gulf of Mexico; over this vast area it is only rare in the west, and only unknown in Colorado, Arizona, and New Mexico (l.c., 278). It is to be observed that the range of *archippus* includes the whole of the area (Canada and the north-eastern States) occupied by the ancestral form *artemis*.

The facts indicate that the changes produced by the invaders were wrought in the conspicuous pattern of a dominant indigenous species, and that the transformed butterfly having adopted the

¹ See also the mimetic resemblance to *L. astyanax* described on pp 189 91.

advertisement of the still more unpalatable *Danaida*, became even more dominant and gained a far wider range than before. The mimetic resemblance arose in a species which we have reason to believe possessed warning colours and some form of special protection before the change occurred. There is no evidence that the special protection was diminished after the assumption of Mimicry, and, if it remain, the new appearance is still a warning character, only one that is learnt by enemies more readily than the old because of the wide advertisement given to it by *Danaida plexippus*. The facts harmonize with the theory of Fritz Müller rather than with that of H. W. Bates.

THE 'POISON-EATING' SWALLOW-TAIL BUTTERFLIES (PHARMACOPHAGUS) AS MODELS FOR MIMICRY

The late Erich Haase gave the name of *Pharmacophagus* or 'Poison-eater' to the section of swallow-tail butterflies whose larvae feed upon *Aristolochia* or allied species, and he made the probable suggestion that the qualities which render them distasteful are derived from the juices of the food-plant. The poison-eating swallow-tails are abundant in tropical America and the Oriental Region, but with the exception of *antenor* in Madagascar are wanting from the Ethiopian Region. They are extensively mimicked by swallow-tails of the other two sections:—*Papilio*, of which *machaon* may be taken as a type, and

Cosmodesmus, of which *podalirius* serves as an example. The distinction between these three sections of *Papilionidae* extends to larval and pupal stages, as was originally discovered by Horsfield. It was made the basis of Haase's classification,¹ recently confirmed and amplified by Rothschild and Jordan.² The latter authorities propose the names 'Aristolochia Swallow-tails', 'Fluted Swallow-tails', and 'Kite Swallow-tails', respectively for Haase's sections *Pharmacophagus*, *Papilio*, and *Cosmodesmus*.

The *Pharmacophagus* swallow-tails are not so well known as models for Mimicry as are the *Danainae*, *Acraeinae*, &c., and it is therefore expedient to say a few words about the section before considering the effect produced by one of its members in North America.

In tropical America not only are the species of *Pharmacophagus* extensively mimicked but Mimicry is also strongly developed within the limits of the section itself, viz. between the two dominant groups *Aeneas* and *Lysander*. In these groups the males are commonly very different in appearance from the females and frequent more open habitats such as the banks of rivers, &c., the females being found in the forest. In the internal Mimicry between *Aeneas* and *Lysander* the males resemble the males, the females the females, but the female patterns are alone extensively mimicked

¹ *Researches on Mimicry*, Pt. ii, Stuttgart, 1896, English translation.

² *Nor. Zool.*, xiii (1906), 411-752.

by other groups—*Papilio*, *Cosmodesmus* and certain *Pierinae*. I have as yet only come across a single example (a *Cosmodesmus*) in which the pattern and green markings of the males are mimicked. One or two species (e. g. *Ph. hahneli*) of *Pharmacophagus* are themselves mimics of dominant Ithomiine genera.

It has already been pointed out on p. 137 that in the *Papilio* mimics of *Pharmacophagus* the resemblance is often attained by the females alone, a tendency exemplified in North America as shown on pp. 181–4. In *Cosmodesmus*, on the other hand, where the Mimicry of these models reaches a far higher level of perfection, it is equally pronounced in both sexes. In Africa, on the other hand, where, in default of *Pharmacophagus* models, the swallow-tails of both groups frequently mimic *Danainae* and *Acracinae*, the resemblances attained by *Cosmodesmus* are far less striking than those of the other section; yet the relationship of Mimicry to sex remains unchanged.

In the Oriental Region the female Mimicry of *Pharmacophagus* is still characteristic of *Papilio*, also appearing in certain *Cosmodesmus* mimics of *Danainae*. Two remarkable features appear in this Region: (1) the development within *Pharmacophagus* of the gigantic Ornithopteras which do not appear to be mimicked at all; (2) the appearance within the section *Papilio* of groups which are mimicked as extensively, perhaps even more extensively, than *Pharmacophagus* itself. Among

the mimics of these *Papilios* are not only species of other groups in the same section but also, although in small proportion, Satyrine butterflies and day-flying moths.

The fact that *Pharmacophagus* and certain groups of *Papilio* should be mimicked pre-eminently by other *Papilionidae* is evidence that Mimicry is most easily attained when there are initial resemblances of size, shape, habits, and modes of flight upon which to build.

PHARMACOPHAGUS (PAPILIO) PHILENOR, L., AS A MODEL FOR MIMICRY IN NORTH AMERICA

Pharmacophagus is a tropical assemblage, but a few species have found their way into the northern belt in both the Old World and the New. *Pharm. polydamas*, with an immense range in South and Central America, also extends into the northern continent but does not there become the object of Mimicry. *Pharm. philenor*, ranging through Mexico and the United States (except the central district from Colorado northwards) but only as a straggler in New England and southern Canada, is on the other hand an important model for Mimicry.

There is here no such interesting history of past migrations to unfold as we were able to trace in the American *Danaidas*. *Ph. philenor* is a member of the distinctively New World species of *Pharmacophagus*, associated together and separated from the Old World species by structural

characters. Rothschild and Jordan state that every species can be recognized as American by the examination of a single joint of one leg, and they are therefore justified in concluding that all the New World species were derived from a single ancestor possessing this character. There is no sufficient evidence that any of the numerous patterns are ancestral as compared with the others, although it is tolerably safe to conclude that the presence of hind-wing 'tails' is primitive as compared with their absence. Following this indication, we find that as a general rule the specialized and modern forms are predominant nearer to the Equator, the comparatively ancestral tailed forms occurring in latitudes more remote from it both north and south.

Ph. philenor is a 'tailed' form, although its subspecies *orsua* in the Tres Marias Islands is nearly tailless. It is probably an intruder into North America from the tropics of the same Continent. It is well known to possess the characteristics of distasteful species—gregarious larvae, tenacity of life, and a strong, disagreeable scent.

THE THREE PAPILIO MIMICS OF PH. PHILENOR IN NORTH AMERICA

The three swallow-tail mimics of *philenor* belong to separate groups of Haase's section *Papilio*. All of them range from the Atlantic to the Mississippi basin.

The female of *Papilio polyxenes asterius* (Cr.) belonging to the MACHAON GROUP mimics *philenor* on both surfaces, the male on the under surface alone, except at Guerrero, Mexico, where a form (*ampliata*) mimetic on the upper surface is transitional into the ordinary male.

Papilio glaucus glaucus (L.) belongs to the GLAUCUS GROUP, next but one to the group containing *asterius*. The female is dimorphic, one form resembling the male and the other (the *turnus*¹ form, mimetic of *philenor*) becoming commoner in the southern part of the range. In the closely allied sub-species *P. glaucus canadensis* (Rothsch. and Jord.) the mimetic female form is unknown.

Papilio troilus troilus (L.) belongs to the next succeeding TROILUS GROUP, allied to the tropical and highly mimetic ANCHISIADES GROUP, with gregarious larvae. Both male and female of *troilus* mimic *philenor* on both wing surfaces.

The most remarkable fact about these three mimics is not their moderate resemblance to the primary model *philenor*, but their extraordinary likeness to one another. Upon the wing or at rest at a little distance they would be indistinguishable, and even in the cabinet they may be easily confused. It is to be expected that the species of allied groups, with patterns converging towards that of a single model, and approaching it by variations which tend to be produced in the

¹ The species is commonly called *P. turnus* and its mimetic female the *glaucus* form. I follow Rothschild and Jordan in transposing these names.

section to which they belong, should incidentally approach one another. But the strong likeness between the mimetic forms of *troilus*, *asterius*, and *glaucus* seems to require something more than this, and supports the conclusion that there is secondary Mimicry between the mimics themselves. It is not necessary to repeat here the details of these secondary resemblances,¹ and as a matter of fact the likeness itself is stronger than might be inferred from a consideration of the details themselves. It is necessary to see it in order to appreciate it.

It is probable that *troilus*, mimetic in both sexes, is the oldest mimic; *asterius*, non-mimetic on the upper surface of the male or with very rough incipient Mimicry, the next to appear; and *glaucus*, mimetic in only one form of the female, the youngest. These conclusions as to relative age are on the whole supported by the relative strength of the detailed resemblances to *philenor* in the three mimics.

In attempting to trace the past history, here again we have the great advantage of knowing the more ancestral patterns from which the three mimics were derived:—*troilus* from a *palamedes*-like form; *asterius* from the pattern of its male, which again leads back to the typical pattern of the MACHAON GROUP; the *turnus* female of *glaucus* from the male and non-mimetic female of the same species.

¹ See *Trans. Ent. Soc. Lond.* (1908), 467-71.

It is highly probable that the earliest steps in the direction of Mimicry in *asterius* and *glaucus* were favoured by the appearance of partially melanic varieties of the female, thus effecting suddenly that essential change which enables a butterfly with a yellow ground-colour to become the mimic of one in which it is black. But this transformation, immensely important as it is, supplies nothing more than a tinted paper for the new picture. That the melanic varieties were partial is clearly shown by the persistence (in *glaucus*) in a subdued and inconspicuous form of certain ancestral features that do not contribute to the Mimicry, but above all by the retention of every element in the original pattern that can be worked up into the new. By the modification of these elements in form or colour,—often in both form and colour,—the detailed mimetic pattern has been wrought upon the darkened surface.

Valuable confirmation of the history suggested in the last paragraph is to be found in the dark form *melasina* (Rothsch. and Jord.) found in both sexes of *P. polyxenes americanus* (Kollar), extending from North Peru to Colombia and Venezuela. This melanic variety probably represents the darkened form of *asterius* before the initiation of the detailed mimicry of *philenor*. The sub-species *americanus* does not enter the range of *philenor*, and those ancestral elements which have been retained by its melanic form have not developed into the mimetic likeness seen in the more northern sub-species *asterius*.

It is well known that all four species (including *philenor*) fly together. Even in my own limited experience I have taken three of them in adjacent streets on the outskirts of Chicago on the same day (Aug. 10, 1897), and the fourth in the same locality a little earlier (July 28). But precise knowledge of their relative proportions in different parts of their range would be of high interest. Again, *troilus* extends to the North-West Territory of Canada, probably far beyond the area in which *philenor* occurs as a straggler; and it would be very interesting to compare minutely large numbers of such specimens with those from districts where the model is dominant. A similar study should be made of the Canadian specimens of *asterius*, although this species does not extend so far beyond the northern limits of the poison-eating model.

From another point of view the interbreeding of the *turnus* female of *glaucus* with a male from some northern district where *turnus* is unknown or very scarce would be of the highest interest. We should here be able to test whether the Mendelian relationship exists between the parent form and its partially melanic variety further transformed by selection,—not a mere melanic ‘mutation’. I trust that my friend Prof. C. B. Davenport may be able to undertake this experiment at the Cold Spring Experimental Station. I cannot doubt that breeding could be easily carried through two generations in a large enclosed

space exposed to the sun and planted with abundant flowers and the food-plant of the species. It would probably be safe to use Long Island males, while female pupae or the freshly bred females themselves could be readily obtained from further south.

THE EVOLUTION OF LIMENITIS (B.) ASTYANAX (F.) AS A MIMIC OF PH. PHILENOR AND ITS PAPILIO MIMICS

Scudder states that *L. astyanax* 'ranges from the Atlantic westward to the Mississippi Valley, and from the Gulf of Mexico northward to about the 43rd parallel of latitude.'¹ It thus falls entirely within the area of *philenor*. The northern boundary of *astyanax* corresponds with the southern limit of its parent *arthemis*, and Scudder (l. c., 289) considers that they interbreed and that the intermediate form *proserpina*, found along the narrow belt where the two species or sub-species meet, is the resulting hybrid. Both *arthemis* and *proserpina* have been bred from the eggs of the latter. There seems little doubt that *astyanax* is a very recent development from *arthemis* in the southern part of its range,—so recent that the areas of distribution still remain distinct and parent and offspring only meet along a narrow line. It is probable that *archippus* arose in the same manner in part of the area of *arthemis*, but

¹ A closely allied species or probably a form of the same species is recorded by Godman and Salvin from Mexico.

that later, after the separation had become complete, it spread northward over the whole range of its parent.

The evolution of *astyanax* from *arthemis* was far simpler than that of *archippus*. The great difference in appearance between parent and offspring is brought about, as regards the upper surface, by the disappearance of the broad white band of *arthemis* together with all but a trace of the sub-apical white markings of the fore wings. Over and within the area formerly occupied by the white band a bluish or greenish iridescence spreads from the marginal region where it exists in *arthemis*. This marginal iridescence—just as in *astyanax*—is bluish in some individuals of *arthemis*, greenish in others. Reddish sub-marginal spots, although rarer in the hind wing of *astyanax*, are actually commoner in the fore wing than in *arthemis*. This curious fact, together with the evidence that *astyanax* and *archippus* may occasionally interbreed, suggests the possibility of some connexion between the origins of the two mimics.

The under surface of *astyanax* has not only similarly lost the white markings, but the chocolate-brown ground-colour of *arthemis* has become transformed into a dark iridescent greenish-brown. Against this background the reddish spots near the margin and base of the wings become far more conspicuous than in the parent form. The material for this transforma-

tion in tint is still to be seen in the great variation of the ground-colour in *arthemis*.

Although, as Scudder rightly maintains (l. c., 287), *L. astyanax* is a very poor mimic of *Pharm. philenor*, it bears considerable resemblance to the three *Papilio* mimics, especially *troilus*. Although the iridescent blue or green of its upper surface approaches rather more closely than the *Papilios* to the brilliant, steely lustre of *philenor*, it is still in this respect widely separated from the primary model and near to the mimics. The reddish spots of the under surface offer but a rough likeness to those of any of the above-named species, but there can be no doubt that their emphasis is an element in the mimetic resemblance.

A careful examination of large numbers of *astyanax* from the extreme south of the range where it passes out of the area of *glaucus* and *troilus* but remains within that of *philenor* and *asterius*, might yield interesting results. An investigation of the proportion it bears to the four *Papilionidae* in various parts of their common range would also be of deep interest. Of the highest importance would be the attempt—which would probably be successful—to breed *astyanax* and *arthemis* and to ascertain whether the Mendelian proportions appear in the offspring of the hybrids. The pairing of *astyanax* and *archippus*, although in this case failure is probable, ought also to be attempted.

THE FEMALE OF ARGYNNIS (SEMNOPSYCHE)
DIANA (CR.) A MIMIC OF LIMENITIS ASTYANAX

The comparatively narrow range of this species is, as Scudder points out, wholly included within that of *astyanax* (l. c., 1802). The Mimicry is confined to the upper surface, where the blue tint has even less sheen than that of any other member of the group clustered round the brilliant *philenor*. Apart from the blue expanse, which he admits to be mimetic, Dr. F. A. Dixey considers that the female of *diana* belongs to a set of dark female forms well known in *Argynnis*, forms which he believes to be ancestral.¹ It is probable that 'the recent evolution of *L. astyanax* provided this ancestral form with a model which it could approach by small and easy steps of variation'.²

THE BEARING UPON THEORIES OF MIMICRY OF
PHARM. PHILENOR AND ITS MIMICS

Haase, who always shows an imperfect appreciation of the scope of Fritz Müller's principle, apparently regarded all the species mentioned in the preceding section as simple Batesian mimics of *philenor*, neglecting the mimetic relationships between the mimics themselves. This interpretation is unconvincing, and most naturalists will agree with Scudder in his hesitation to accept the two Nymphalines, *astyanax* and *diana* (female), as simple mimics of *philenor*. The Müllerian

¹ *Trans. Ent. Soc. Lond.* (1890), 89-129.² *Ibid.* (1908), 475.

hypothesis at once explains relationships that are mere coincidences under that of Bates.

Pharm. philenor, a probable intruder from the American tropics, produced its effect upon the three large *Papilios*—butterflies with a conspicuous under surface pattern, in large part reproducing that of the upper surface, butterflies belonging to a section that provides models for extensive Mimicry in the Oriental Region. They may be regarded as Müllerian Mimics of the primary *Pharmacophagus* model, exhibiting a certain amount of Secondary Mimicry of one another.

The four above-named *Papilionidae*, but especially the three mimics acting as secondary models, then produced an effect upon *L. arthemis*—that same conspicuous, specially defended element in the North American butterfly fauna which was influenced in an entirely different direction by the Danaine invaders. The result of the former influence is seen in *L. astyanax*, a secondary mimic of the three *Papilio* mimics of *philenor*.

One of the most interesting elements in this complex mimetic system is the final appearance of a tertiary mimic of *astyanax*, viz. the female of *Argynnis diana*. This was recognized by Scudder, although, not fully appreciating the Müllerian hypothesis, he was much puzzled by the fact.¹

The under surface of the female *diana* is inconspicuous, and, considering also the restricted

¹ l. c., 718, 1802 see, however, 266, where Scudder suggests that *astyanax* may possibly be specially protected.

range and relative rarity of the species, it is probable that this member of the assemblage of species convergent round *philenor* is a Batesian mimic. But its resemblance to *astyanax* supports the conclusion that this latter and the sister-species *archippus* (and its forms) are Müllerian mimics and the parent *arthemis* a specially protected species. The resemblance of *astyanax* to the three species of the section *Papilio*, as well as the secondary resemblances between the three, similarly supports the conclusion that these mimics are Müllerian.

I have not hitherto called attention to the paramount need for experimental research and field observations directed to test for the presence of distasteful qualities and to estimate their effect upon enemies of the most varied kinds. It is of the utmost importance that such investigations should be undertaken on the largest possible scale. In the meantime the Müllerian Hypothesis appears to explain a series of remarkable relationships which remain coincidences under any other hypothesis.

THE RESEMBLANCES BETWEEN LIMENITIS
(ADELPHA) CALIFORNICA (BUTL.) AND LIMENITIS
(NAJAS) LORQUINI (BOISD.)

The examples of Mimicry which we have been considering hitherto are, with the exception of the widespread *L. archippus*, characteristic of the eastern side of North America. The present

instance, the last of the examples known in this portion of the northern land-belt, is found on the Pacific coast. The resemblances are somewhat crude but of quite remarkable interest.

Limenitis californica, because of its pattern and colouring, is often placed in *Adelpha*, a large genus with over seventy species all confined to tropical America. *Adelpha* is separated from the closely allied northern genus *Limenitis* by the hairiness of the eyes in front. *Californica* is by this character as well as its more northern range associated with the heterogeneous assemblage '*Limenitis*', which so much requires a thorough revision. In adopting this view I accept the position assigned to the species by Scudder in 1875.¹

Closely allied to *californica*, of Oregon, California, and Nevada, is *L. bredowi* (Hübner) of Arizona, Mexico, and Guatemala. A much needed investigation is the determination whether these two forms meet, and interbreed along the line of contact.

The southern species or sub-species *bredowi*, is associated in Mexico and Guatemala with many true species of *Adelpha* of which no less than thirty-one extend into Central America. To these it, and to a less extent the northern *californica*, bear much likeness, especially to *A. dyonysa* (Hew.), *massilia* (Feld), *lerna* (Hew.), and *fessonia* (Hew.). This likeness is probably a mimetic resemblance which extends beyond the

¹ *Bull. Buffalo Soc. N. Sc.* (Feb., 1875), 233.

range of the models into Arizona, and, with diminished effect, still further north into the allied sub-species. Although the details of the resemblance leave little doubt that this interpretation is correct for the southern *bredowi*, it is possible that *californica* represents an ancestral form connecting the *Adelphas* with *Limenitis*, a form left isolated and comparatively unchanged in the north,¹ while its southern allies have been modified by the presence of the dominant *Adelphas*. At any rate in one feature neither sub-species appears to be mimetic, viz. in the yellowish tint of the conspicuous band crossing both wings; for in all the Central American *Adelphas* at all resembling them this marking is pure white or bluish-white. We cannot hope to determine how far the pattern of *californica* is ancestral until the structural relationships and the early stages of *Limenitis* in the widest sense and *Adelpha* have been most minutely investigated.

Limenitis lorquini, occurring with *L. californica* in Nevada, California, and Oregon, also extends far north of this species into British Columbia and Vancouver Island. Among all the North American species of *Limenitis* it is the one which comes nearest to the Old World forms, as Scudder recognized when he included it with the European *L. populi* in the genus *Najas*, separating all the other American forms of *Limenitis* except cali-

¹ See, however, pp 198-9.

forinica and *Basilarchia*. Even such fleeting characters as the markings show the Old World affinities of *lorquini* in the strong development of the pale spot in the fore wing cell and the position and form of the pale band crossing both wings. It is to be noted furthermore that its distribution, and especially its extension northward, along the Pacific coast, bring *lorquini* into closest proximity to the Old World species.

In certain important respects the upper surface pattern of *L. lorquini* is certainly mimetic of *californica*:—

The conspicuous fulvous apical area of the fore wing; the yellowish tint of the band crossing both wings; and, although here the interpretation is less certain, the fulvous marking at the anal angle of the hind wing.

1. In the first and most important of these points of superficial resemblance there is, so far as my experience goes, a much greater average development of the fulvous patch in specimens of *lorquini* which enter the range of *californica* in Oregon and California than in those which come from Canada, entirely beyond the range of the model.

The close relationship between *californica* and *lorquini* may incline naturalists to look on their resemblance as due to affinity and not to Mimicry. 'It is commonly forgotten that mimicry, being *independent* of affinity, occurs between forms of all degrees of relationship, the closest as well as

the most remote';¹ although of course the latter are easy to interpret, while the former may be excessively difficult. In this case, however, there is neither doubt nor difficulty, for not only is there the geographical coincidence between the model and the average increase of the marking in the mimic, but the fulvous apical marking of *lorquini*—of a somewhat richer, deeper shade than the tawny patch of *californica*—is due to the inward growth of a marginal marking, while that of the model occupies a clearly defined sub-marginal and sub-apical position. The resemblance is, in fact, produced by markings which are essentially different; yet in some of the southern examples of *lorquini* in which the markings extend inward to the greatest distance the superficial resemblance is very considerable.

The above-stated conclusion that the chief mimetic element of *lorquini* is on the average subject to considerable strengthening in the southern part of its range, is founded on an examination of the few dozen specimens I have been able to study in English collections, and especially the Godman-Salvin material in the British Museum. I now trust that the subject may be taken up by American naturalists and many hundreds of specimens compared from all parts of the north and south range of the species.

2. In the second point also, the yellowish tint

¹ *Trans. Ent. Soc. Lond.* (1908), 482.

of the principal band, the resemblance is certainly mimetic and not due to affinity; for *lorquini*, ancestral in certain other features, has here lost the original whiteness of this marking, preserved not only in the Old World but in *Limenitis arthemis* and *L. weidermeyer*i (Edw.) of the New. An excessively slight deepening of the yellow tint could be made out in southern individuals from the area occupied by the model. In order to detect the difference, a long series of northern specimens should be placed beside a similar series from the south and the two compared in a strong light. But far larger numbers than I have seen ought to be examined from this point of view, and, if it were possible to make it, the comparison of perfectly fresh specimens would be most desirable.

3. The fulvous marking at the anal angle of the hind wing is excessively variable and often absent from specimens in all parts of the range. The comparison of a very large amount of material is necessary before we can reach any safe conclusions as to the existence of mimetic resemblance in this feature, and the same is true of the extremely variable under surface of *lorquini*, in which the development of the inner row of sub-marginal bluish lunules may be mimetic of *californica*. This feature was generally suppressed in the Vancouver Island specimens I have seen.

We now come to the consideration of certain

differences between *L. californica* and its southern form *bredowi* which promote a likeness to *lorquini*. If these are not mere coincidences, we can hardly escape the conclusion that there is Reciprocal Mimicry (Diaposematism) between *californica* and *bredowi*.

1. The wings of both sexes of *californica* are more rounded than those of the males of *bredowi*, in this respect resembling both sexes of *lorquini*. The fact that the southern females have rounded wings may indicate that this character is ancestral in both sexes, the males alone having been modified in Mimicry of *Adelpha*. But it is a probable hypothesis that the presence of *lorquini* has prevented this mimetic feature from passing northward into the males of *californica*. It does pass far beyond *Adelpha* in the northernmost part of the range of *bredowi* in Arizona.

2. The fulvous marking at the anal angle of the hind wing which forms so characteristic a feature of *bredowi*, is greatly reduced in *californica*, approximating to *lorquini*, which in this respect may be advancing to meet its model (see p. 196).

3. The following points concern the band crossing the fore wing. Owing to the small size of the last spot in *californica* and the different direction of the spot next to it, the junction between the bands of fore and hind wing forms a step-like break in *californica*, whereas in *bredowi* the bands tend to be continuous, approximating more closely

to the single smooth streak crossing both wings in the *Adelphas*. In *lorquini* this step-like break and want of continuity in direction is even more pronounced. Again, the fore wing band of *lorquini*—one of its ancestral features—forms, with the adjacent hind wing spot, a drawn-out zigzag like a flattened-down W. By a modification in the position and direction of the spots of *californica* as compared with *bredowi*, it also gains the appearance of a very flattened W, although a far less regular one than that of *lorquini*. The resemblance is only superficial; for corresponding spots do not occupy the upper angle of the W in the two species. But the attainment of a likeness by means that are different from those employed in another species supports the interpretation of the resemblance as mimetic.

Whatever be the true interpretation of the resemblances above described, it is of the utmost importance and interest to study the relative numbers of *californica* and *lorquini* at as many different points as possible in their common range, to observe how far they fly together and present the same appearance on the wing and at rest from a little distance, and to test their relative palatability on a variety of insect-eating animals found in the same area.

The following general considerations support the conclusion that *californica* is not an ancient element in the Pacific fauna of North America, but a comparatively recent intruder from the

south—an intruder that has modified the indigenous inhabitant *lorquini* and has been also reciprocally modified thereby.

Limenitis in the broad sense is part of the ancient northern butterfly fauna of North America. It has here split up into several well-marked species characteristic of the area. It is highly susceptible to mimetic influence—far more so than any other North American group—and contributes the majority of the examples of Mimicry from this part of the world. *L. archippus* has been shown to be the result of a recent invasion,—its southern and eastern forms to be still newer products of the changes in *archippus* itself. The sensitiveness of the group is shown by the fact that, in spite of this recent origin, all except *astyanax* are most beautiful and striking mimics; and even *astyanax* is a better mimic than *lorquini*. The fact that *lorquini*, the member of so sensitive a group, is an undoubted mimic, but a very poor mimic, supports the conclusion that the association with its model has endured for but a brief period, a conclusion also supported by the diminution of the resemblance outside the range of *californica*.

If the relationships which I have found to exist in the available material—in quantity very insufficient for such minute comparisons—if these are confirmed by extensive investigations in America, it will follow that the resemblances between *L. californica* and *L. lorquini* will be one

of the most interesting and instructive examples of Mimicry in the world. Its value will lie in the early stage reached by the resemblance, together with the diminution of the likeness in *californica* to the south and, especially, in *lorquini* to the north. There is no reasonable doubt that *lorquini* forms a single Syngamic community along the Pacific coast of North America, and we should therefore witness, first, the marked strengthening of characters in an area of selection; secondly, their transmission with diminished effect into other areas.

If what I have observed be the phenomena presented by the growth, at an early stage, of a mimetic likeness in *lorquini*, then that growth is 'continuous' and transitional to the last and finest degree.

It is perhaps appropriate to state in a few lines how we may imagine that the selection of minute characteristics such as the presence or the position of a single spot may be made. We ourselves may observe that one individual butterfly is a better mimic than another. We may then analyse the pattern, as I have attempted to do in this address, and realize that the improvement is due to differences in one or more relatively minute elements. Recognizing the cause of the change, we are perhaps prone erroneously to suppose that enemies recognize it also and that selection has been brought to bear directly and consciously upon it. Such a view is almost cer-

tainly wrong. The only probable hypothesis is that sharp-sighted enemies, without analysing the markings, recognize differences in degrees of likeness, and that the selective pressure exercised by them is influenced by the recognition.

A great deal of attention is rightly directed at the present day to the value of experiment, and indeed it is impossible to over-estimate its importance. But while human performance is of the deepest interest for the solution of mysteries innumerable, of more profound significance still, for the comprehension of the method of evolution, is the vast performance of Nature herself.¹ Because of the bright promise it holds for the understanding of Nature's experiments, I have brought before you the subject of Mimicry in North American butterflies.

In the introductory words I spoke of the relationship of my subject to the teachings of Darwin, and now I am anxious to connect this address by a closer link to the personality of the illustrious naturalist. With the kind consent of Mr. Francis Darwin, I am able to achieve this object by printing, for the first time, a letter, recently discovered in the archives of the Hope Department at Oxford, written by Darwin to the Founder in 1837. It is concerned with the insect material collected on

¹ See Carl H. Eigenmann in *Fifty Years of Darwinism*, New York (1909), 208.

the *Beagle*, and is of peculiar interest because so few of Darwin's letters of this early date have been preserved. The letter clearly exhibits the keen interest which Darwin took in the working out of his collections, and the free and generous use he made of his material. A number of Diptera captured by him in Australia and Tasmania—evidently gifts to Mr. Hope—exist in the Hope Department, and are still in excellent condition. It is probable that species of other groups collected by him are also present.

DEAR HOPE

I called yesterday on you and left a tin box with a few Hobart Town beetles, which I had neglected to put with the others. Is not there not [*sic*] a *Chrysomela* among them, very like the English species which feeds on the Broom.—I have spoken to Waterhouse about the Australian insects; you can have them when you like.—The collections in the pill boxes come from Sydney, Hobart town, and King George's Sound.—Do you want all orders for your work? Some are already I believe in the hands of Mr. Walker, and you know Waterhouse has described some minute Coleoptera in the papers read to the Entomological Soc: To these descriptions of course you will refer.—You will be glad to find that many of the minute Coleoptera from Sydney are mounted on cards.—Will you send me as soon as you conveniently can, one of my boxes, as I am in want of them to transplant some more insects.—Perhaps you had better return the Carabi, as they came from *several* localities I am afraid of some mistake. We must put out specimens for the Entomolog: Soc: and your Cabinet. May I state in a note on your authority that a third or a half of the insects which you already have of mine from Sydney and Hobart town are undescribed.—It is a striking fact, if such is the case, for it shows how imperfectly known

the insects are, even in the close neighbourhood of the two Australian Capitals.

Floreat Entomologia

Yours most truly

Wednesday.

CHAS. DARWIN.¹

The last words of Darwin's letter are surely a most fitting conclusion to this Anniversary address, and I conclude by quoting his humorous repetition of them probably twenty years later.

“Floreat Entomologia”!—to which toast at Cambridge I have drunk many a glass of wine. So again, “Floreat Entomologia.” N.B. I have *not* now been drinking any glasses full of wine.’²

CONCLUSIONS

It will probably be convenient to sum up rather fully the chief conclusions contained in the foregoing address.

1. The study of Mimicry possesses special advantages for an understanding of the history and causes of evolution.

¹ The letter is addressed: ‘The Revd. F. W. Hope, 56, Upper Seymour Street.’ At the head Mr. Hope had written ‘D’, and the date ‘1837’. The red-stamped post-mark gives the date ‘Ju. 22, 1837’. Darwin's own address (36, Great Marlborough Street) does not appear. At the date of the letter the Entomological Society of London possessed a large collection of insects, long since dispersed. Darwin knew Mr. Hope before the Voyage, and speaks in letters to W. D. Fox (1829–30) of his splendid collection and of his generosity with specimens. He also went for an entomological trip in North Wales with Hope (June, 1829), unfortunately broken short for Darwin by ill health. See *Life and Letters*, i. 174, 175, 178, 181. G. R. Waterhouse and Francis Walker referred to in the letter, were both on the staff of the British Museum.

² To Sir John Lubbock (Lord Avebury), some date before 1857—*Life and Letters*, ii. 141.

2. North America is the most suitable area in the world in which to begin the study of Mimicry.

3. The great American Danaine butterflies, formerly included in the genera *Anosia* and *Tasitia*, are a foreign element in the New World fauna. They bear the closest affinity to a large group of indigenous Old World *Danainae*, and should be fused with the nearest of these (*Limnas* and *Salatura*) into a single genus, *Danaida*.

4. The Old World origin of *Danaida* is also proved by the extent and variety of its mimetic relationships; while the path of its invasion of the New World and of South by way of North America, may be traced by foot-prints, as it were, of mimetic effect.

5. That *Danaida plexippus* is the older invader is equally shown by the depth of the impression it has made and the amount of change it has itself undergone in the New World.

6. *Danaida berenice* and its form *strigosa* show comparatively slight changes in the New World, and, as regards mimetic influence, have but deepened the foot-prints left by *plexippus*.

7. *Limenitis arthemis*, the indigenous ancestor of the mimic of *plexippus*, persists with little or no change; and it is possible to show how far the very different markings of the mimetic daughter-species, *L. archippus*, have been carved out of those of the parent.

8. The recent date of this great superficial transformation is proved by the close resemblances

between the larval and pupal stages of parent and offspring. *L. archippus* also probably occasionally interbreeds with the mimetic *L. astyanax*—a still younger descendant of the same parent.

9. *L. archippus* probably arose on the southern borders of *arthemis*, but afterwards ranged northwards over the area of the parent species.

10. The southern *astyanax*, meeting the northern *arthemis* along a narrow belt, is probably repeating the earlier history of *archippus*.

11. The forms or sub-species of *archippus*—*floridensis* in Florida and *hulsti* in Arizona—have arisen from the earlier mimic of *D. plexippus* as a result of the predominance in these localities, respectively, of *Danaida berenice* and its form *strigosa*.

12. Details of the older Mimicry persist in *floridensis* (and perhaps in *hulsti*), somewhat detracting from the newer resemblance.

13. Certain features in the mimetic likeness newly attained in Florida and Arizona are probably due to the recall or the re-emphasis of elements in the pattern of *arthemis* which had been greatly reduced in *archippus*.

14. The fact that the invading *Danaidas* have only influenced, among the whole indigenous butterfly fauna, the dominant conspicuous Nymphaline genus *Limenitis*, supports a Mullerian as opposed to a Batesian interpretation of the phenomena.

15. The fact that the ancestral pattern of a species indigenous in the temperate zone of the New World should be wholly transformed by

a recent invader from the Old World tropics—the invader meanwhile retaining its original characteristic pattern,—is demonstrative of the inadequacy of the theory which refers these likenesses to the influence of soil, climate, &c.

16. The poison-eating ‘*Aristolochia* swallow-tail’ *Pharmacophagus* (*Papilio*) *philenor* belongs structurally to the American division of this tropical section, and is probably an intruder into North America from the south.

17. Just as tropical species of *Pharmacophagus* are mimicked, especially by other sections of swallow-tails, so the invading *philenor* is mimicked by three species of the section ‘*Papilio*’.

18. Of these three—*Papilio troilus*, mimetic in both sexes, is probably the oldest; *P. asterius*, mimetic in female and on under surface of male, the next; and *P. glaucus*, mimetic in one out of the two forms of female (the mimetic form becoming more numerous in the south of the range), the youngest.

19. The ancestors of these mimics persist with little or no change—in the two last-named species, the non-mimetic sex or form; in the first-named, the allied *palamedes*. By their aid we can reconstruct the history of the transformation.

20. In *asterius* and *glaucus* partially melanic forms of the female probably supplied a tinted background on which the new and mimetic picture was gradually built up by the modification of elements in the original non-mimetic pattern.

21. The close resemblance between the three mimicking species cannot be entirely explained by their convergence upon a single model, but seems to imply the existence of Secondary Mimicry between them.

22. *Limenitis astyanax* has arisen as a very recent modification of *arthemis* in Mimicry of *philenor*, and especially in Secondary Mimicry of the three *Papilio* mimics.

23. The female of *Argynnis* (*Semnopsyche*) *diana* has arisen as a tertiary mimic, on the upper surface, of *L. astyanax*. Its under surface, inconspicuous when contrasted with that of the male, suggests that the species is palatable as compared with the rest of this combination and that its Mimicry is Batesian.

24. The dark ground and pale markings of the female *diana* are probably analogous with those of other dark female forms in *Argynnidae*, while the blue colouring is an additional feature of purely mimetic significance.

25. The arrangement of the North American butterflies which converge on *Pharm. philenor*, in concentric rings each mimetic of that lying within it, strongly supports a Mullerian interpretation of all except the species (*diana*) in the outermost layer.

26. *Limenitis* (*Adelpha*) *californica* of the Pacific coast is probably a *Limenitis* mimic of the South American genus *Adelpha*, to which its southern sub-species *bredowi* bears a stronger resemblance.

27. *Limenitis (Najas) lorquini*, in some respects the most ancestral of the North American species of the group, is in other respects a mimic of *L. californica*.

28. Certain features in which *lorquini* superficially resembles *californica* are on the average more strongly developed in the area where the two species overlap, while they diminish when *lorquini* passes northward of this area.

29. The differences between *bredowi*, ranging entirely south of *lorquini*, and *californica* are such as to promote a superficial resemblance between the latter and *lorquini*, supporting the hypothesis that the resemblances between them have been caused by reciprocal approach (Diaposematism).

30. The differences which distinguish *bredowi* from *californica* are such as to promote a resemblance to the tropical American genus *Adelpha*. They are retained by *bredowi* in Arizona, north of the range of any true *Adelpha*.¹

31. The detailed study of these resemblances on the Pacific coast of North America leads to the conclusion that the Mimicry is in an incipient stage and that it has been reached and is probably still advancing by minute increments,—that the evolution is ‘continuous’ to the last degree.

32. In addition to their bearing upon the problems of Mimicry, the examples considered

¹ In the southernmost part of the range of *bredowi*, in Guatemala, the resemblance to *Adelpha* was very slightly augmented in the only two specimens from this locality I have had the opportunity of studying (*Trans. Ent. Soc. Lond.*, 1908, 485).

in the address afford some of the very best material for testing the operation of Mendel's Law under natural conditions.

I wish again to caution my readers that the above conclusions have been drawn from the careful study of a limited number of examples. Although insufficient in quantity, the English material is as a whole excellent in quality. Thus, many of the Pacific coast specimens were captured by Lord Walsingham, Dr. F. D. Godman, and Mr. H. J. Elwes, and the geographical data are of course as full and precise as we should expect or wish.

I trust that my brother naturalists in America will make a determined attack on the fascinating problems offered by the phenomena of Mimicry in the North American butterfly fauna. In this favoured part of the world the problems have been seen to be sharp and clear as compared with the almost infinite complexity of the tropics. If my assistance or advice be of any value it is always at the service of those who desire to undertake such investigations.

It has been abundantly shown in the course of the address that immense numbers of specimens are required from the most varied localities; and it is likely that difficulties may be presented by the necessary manipulation, labelling, convenient arrangement, and permanent preservation for the study of future as well as living natural-

ists, of so large a mass of material. I shall, however, be most pleased to undertake this part of the investigation as regards all specimens accompanied by adequate data of space and time. Such material, preserved in the Hope Department, may be readily compared with the ever-increasing mass of examples illustrating the same principles in other parts of the world. If the indications observed in a small series are still found to hold in a large one, the growth of such a feature as the orange-brown apex of the fore wing in *Limenitis lorquini* would be demonstrated by a glance at its average condition in specimens from the different localities as we pass from north to south. Furthermore, we might reasonably hope that a similar series collected after an interval not greatly prolonged would exhibit differences in average composition—the actual measurable evidence of the evolution of a character in a species in the natural state. Even though such evidence be left for our successors to witness, it still remains our duty to provide them with the standard by which alone they will be able to detect and measure it. But I am hopeful of more than this, and think it by no means unlikely that a part of the reward may be reaped by a single generation of workers.

An excellent example of work done in a single locality is afforded by the data obtained by Mr. J. H. Cook, and summarized in the following note.

NOTE.—*The capture of males of L. archippus in which the black stripe was wanting from the upper surface of the hind wing, and of transitional forms of both sexes, at Albany, N.Y., by John H. Cook.*

Mr. Cook first met with the stripeless form in June, 1898, near Hudson, N.Y. A second specimen was captured near his home in Albany in 1901, and a third in the same field in the following year. This latter was a beautiful specimen apparently only just emerged from the pupa. Mr. Cook's attention was now thoroughly aroused and he collected assiduously at Albany during three seasons, always working on the best ground to the west of the city, and taking over 90 specimens with the stripe wholly or nearly suppressed. The following conclusions were reached :—(1) All the stripeless *archippus* captured were males ; (2) The females shared the tendency but never reached the extreme found in the other sex ; (3) Most of the individuals taken showed some weakening of the stripe, varying from a slight break (most commonly between veins III and V_2 and between V_3 and VII_2 , of the system of Comstock and Needham) to complete suppression on the upper surface. (4) At Albany individuals with a broken stripe outnumbered those with an entire stripe in the proportion of about 18 to 1, while stripeless specimens were taken in the average proportion of 1 to 14. Mr. Cook also collected data from other localities and endeavoured to interest correspondents in the problem. Including the Albany material he secured records of about 1600 specimens and was able to reach the conclusion that in New England and the Middle States broken-striped individuals are not uncommon though generally outnumbered by those with a continuous stripe. He did not meet with any record of a perfectly stripeless form except for his own observations and the two specimens to which the name *pseudodorippus* has been given. Strecker's type of this form exists in Dr. W. J. Holland's collection (*Butterfly Book*, New York (1899), 185). These two *pseudodorippus* were also taken in the Eastern States (the Catskill Mountains, and in Massachusetts), but Mr. Cook, who has seen one and received

from Dr. Holland an account of the other, believes that the disappearance of the stripe is here part of a general blurring of the colour-scheme in which some elements are obliterated and there is a tendency towards the invasion of one colour-area by another. The extreme varieties captured by Mr. Cook himself, did not, on the other hand, differ at all from the normal *archippus* except in the absence of the black stripe from the upper surface of the hind wings. To this stripeless variety Mr. Cook and Mr. Watson have given the name *lanthanis*. Mr. Cook's accurate data and most of his specimens were unfortunately destroyed when the college buildings at Albany were burnt down on Jan. 6, 1906. It is much to be hoped that he may be able to continue his most interesting observations in this favourable locality, and that naturalists may be stimulated, by these records, now by Mr. Cook's kindness made public for the first time, to work in other North American localities.

VII

LETTERS FROM CHARLES DARWIN TO ROLAND TRIMEN (1863-1871)

MY friend, Mr. Roland Trimen, Hon. M.A. (Oxon.), F.R.S., was at the Cape when Mr. Francis Darwin's great work was in course of preparation. On this account his fine series of letters has remained unpublished up to the present date. Now, with his kind consent and that of Mr. Francis Darwin, it is a great pleasure to be able to include in this memorial volume a single complete set of letters, moderate in number, but in every way most characteristic of the writer.

Mr. Trimen has very kindly written the following deeply interesting account of his first meeting with Darwin exactly half a century ago. As we read the story, the intense antagonisms at first aroused by the *Origin* seem again to rise into life and activity :--

'It was in the Insect Room of the Zoological Department of the British Museum that I had my first glimpse of the illustrious Darwin. Towards the close of 1859, after my return from the Cape, I spent much time in the

Insect Room identifying and comparing the insects collected with those in the National Collection. One day I was at work in the next compartment to that in which Adam White sat, and heard someone come in and a cheery, mellow voice say, "Good-morning, Mr. White;—I'm afraid you won't speak to me any more!" While I was conjecturing who the visitor could be, I was electrified by hearing White reply, in the most solemn and earnest way, "Ah, Sir! if ye had only stopped with the *Voyage of the Beagle*!" There was a real lament in his voice, pathetic to any one who knew how to this kindly Scot, in his rigid orthodoxy and limited scientific view, the epoch-making *Origin*, then just published, was more than a stumbling-block—it was a grievous and painful lapse into error of the most pernicious kind. Mr. Darwin came almost directly into the compartment where I was working, and White was most warmly thanked by him for pointing out the insects he wished to see. Though I was longing for White to introduce me, I knew perfectly well that he would not do so; and after Mr. Darwin's departure White gave me many warnings against being lured into acceptance of the dangerous doctrines so seductively set forth by this most eminent but mistaken naturalist.

'A little while afterwards, on the same day, I again saw Darwin in the Bird Galleries, where it was, I think, G. R. Gray who was showing him some mounted birds. A clerical friend with me, also a naturalist, curiously enough echoed White's warning by indicating Darwin as "the most dangerous man in England".

'Years afterwards, when I had reached the honour of correspondence and personal acquaintance with Mr. Darwin, I gave him some amusement by my account of the impressive manner in which, on the first day of my seeing him, I had been warned by two

naturalists, much my seniors, to give him a wide berth.' ¹

In working out the various subjects referred to in the letters, I have received the kindest help from Mr. Trimen and Mr. Francis Darwin. Although Mr. Trimen did not keep copies of his own letters, he was able to remember the details of nearly all the questions touched upon in the correspondence, while other data were recovered from Darwin's works. Without Mr. Francis Darwin's help I should have been unable to decipher a few obscurely written words, or to have obtained other information bearing upon the conditions under which the letters were written.

The letters are, as I have already implied, a typical series. They show all the characteristics of Darwin in his relations with younger men who helped him in his work. 'They are,' as Mr. Trimen truly says, 'of value as an additional illustration of one of the most charming and attractive sides of Darwin's character—the gracious and glad welcome and recognition he never failed to extend to every one who even in the slightest degree endeavoured to render some aid in his researches.'

In addition to the full recognition he accorded in his published works, we find, in these letters as in others, that Darwin not only urged his correspondent to publish on his own account,

¹ See p. 219.

but himself arranged the details of publication and assisted in drawing up one of the memoirs. It is easy to imagine the delight and encouragement with which his generous words of praise for every effort would be received, and how infallibly they would become the inspiration to further effort. And with all this stimulus and encouragement there is ever present the warmest sympathy with difficulties of every kind, and the keenest anxiety not to overburden another with trouble or expense. We recognize an unbounded love of nature and of discovery, and the keenest appreciation for the same enthusiasm in another. We feel, again and again, as we read these letters, the presence of the bright, courageous spirit that could pierce the dark shadow of lifelong pain and discomfort, and preserve undimmed its humour and its breadth of view. And the brooding shadow is never accorded the dignity of recognition on its own account, being only revealed because of the veto it had the power to impose—work prevented or long drawn out, interviews with friends cut short or postponed.

For this reason brief notes of invitation, which might otherwise be regarded as trivial, all bear their part in creating the general impression, and the whole correspondence remains untouched and unabridged.

Of the nineteen letters printed in this section of the book, one (No. 18) is from Mrs. Darwin.

Of the remainder, fourteen are holograph letters. by Charles Darwin, one (No. 7) is signed and corrected, while three (Nos. 6, 11, 17) are only signed by him.

The letters are arranged in the order of date. Darwin, as was his custom, omitted to write the year, but fortunately this was nearly always added by Mr. Trimen himself, together with the date at which the letter was received.

Publications and the names of species, &c., although not underlined in the originals, are, for the sake of convenience, printed in italics.

The first series of letters, seven in number, deal with botanical subjects,—especially Orchids, and the inquiries which grew out of the investigations upon them (such as the Peach-perforating moths). These are referred to in all seven letters; *Oxalis* as material for the study of heterostyled flowers in Nos. 3-7; insect visitors to *Asclepiadae*, *Apocynae*, and *Physianthus* in No. 4; the fertilization by birds of *Strelitzia* in Nos. 6, 7.

It will be observed that Darwin in the very first letter began to urge his correspondent to send home the records of observations for publication. His advice and help were very soon accepted, and, in the *Fertilisation of Orchids*,¹ Darwin acknowledged the assistance he had received, and referred to Trimen's papers, in the publications of the Linnean Society, on *Bonatea speciosa* and *Disa grandiflora*, in each case specify-

¹ Second edit., sixth impression (1899), 40, 76-8.

ing briefly the peculiarities of structure which the author had noted as governing access to the nectary, so as almost to compel the removal of the pollinia by insect visitors of the right kind.

1.

Jan. 31st [1863]

DOWN.

BROMLEY.

KENT. S.E.

MY DEAR SIR

I thank you most sincerely for your pleasant letter and M.S. on Orchids. Your sketches seem to me very good, and wonderful under circumstances of their execution. I cannot say how much interested I have been in studying your descriptions. I think I understand all; but these Orchids (except *Eulophia*) are so *surprisingly* different from anything that I have seen that I could hardly make them out for some time and even fancied in some cases that you had miscalled upper sepal and Labellum. But at last I see my way. I am no more a Botanist than you say you are, and I know nothing of any orchids except those seen by me. Therefore I was astonished at the upper sepal being produced into a nectary; even more astonished at stigma standing high above the pollinia &c &c.—How curious is pollinium of *Disperis*!—What beautiful and new contrivances you show, and how well you have studied them! Upon the whole I think No. V. & VI. unnamed (I have sent your drawings to Prof. Harvey to name for me) have interested me most: everything seems to occur in a reversed direction compared with our true *Orchis*.—You do not mention any movement of the pollinia, when attached to an object; and as you are so acute an observer, I infer that there are no such move-

ments; and indeed in those you describe such movements would be superfluous. If you have time to wander about do watch some kinds and see insects do the work.¹ Those with long nectaries would be probably hopeless to watch as probably fertilized by Moths.—But since my publication I have ascertained that with *Orchis*, Diptera are chief workmen.—They certainly do puncture the walls of nectary, and so get juice. *Disperis* would be grand to watch, and discover what attracts insects.—You draw so well, and have so seized on the subject, that you ought really to take up 2 or 3 of the most distinct genera, and watch them, experiment on them by mutilation of parts, and describe them and send over an excellent paper to Linnean Soc^y or some other Soc^y.—I have so much other work, that I hardly know whether I shall ever publish again,—not but what I have already collected some curious new matter; for the subject delights me, and I cannot resist observing.

I am very glad to hear that you do not now think me so dangerous a person!² You will gradually, I can see, become as depraved, as I am.—I believe, or am inclined to believe, in one or very few primordial forms, from community of structure and early embryonic resemblances in each great class.—

With most cordial thanks I remain my dear Sir

Yours sincerely

CH. DARWIN

P.S. Would it be asking too great a favour to beg you

¹ Mr. Trimen writes as follows of his attempts to carry out Darwin's advice: 'I had no success with this, though I watched a variety of orchids as opportunity offered. A good many visitors of various orders came, but they were evidently not regular customers ("unbidden guests," as Kerner says), and I never saw a pollinium actually removed by any one of them.'

Trimen found, however, that one or both pollinia had been removed from 12 out of 78 flowers of *Disa grandiflora* — *Fertilisation of Orchids* (1877), 78.

² See pp. 214–15.

to put 2 or 3 flowers of *Satyrium* or your No. V. or VI. in bottle with spirits and water, and send home by any opportunity. I would then compare your drawings and add some remarks on your authority, if I ever publish again.—But I hope, what will be much better, to see a paper by yourself.

If you come across *Bonatea* pray study it—it seems most extraordinary in description.—

2.

Feb. 16th[, 1863.]

DOWN.

BROMLEY.

KENT. S.E.

DEAR SIR

I have thought you would like to see copy enclosed of letter by Prof. Harvey giving names of your two orchids, Pl. V. and VI, which were unnamed.¹—Now that I hear that in *Satyrium* the nectaries belong to the true Labellum;² the relation of the parts is to me very puzzling: discs, pollen-masses and stigmatic surface seem all on the wrong side.—If you pursue the subject, I hope you will observe whether there is any relation

¹ The copy of W. H. Harvey's letter (dated Feb. 3, 1863, Trin. Coll., Dublin) states concerning the two unnamed forms: 'Both are of the large genus *Disa*, and I feel confidence in calling them (Pl. V) *D. barbata* and (Pl. VI) *D. cornuta*, both common near Capetown.'

² The copy of Harvey's letter contains the following account: 'Nectariferous back sepals are quite frequent among Cape Orchids—and correspondently depauperated labella. The labellum is often a mere little tongue [sketch]—sometimes a mere thread [sketch]—and sometimes as in *Brownleia*, nearly disappears altogether, and is adnate to the column.'

'In *Satyrium* the two spurred affair is a true labellum—the sepals and petals small and crowded together at the front of flower—the opposite to *Disa*'

(as in English Orchids) between the rapidity of the setting of the viscid matter and nectar being stored ready for suction or confined in cellular tissue.—

I was at Kew 2 or 3 days ago and was telling Dr. Hooker and Mr H. Gower of your work: they expressed a strong wish to try whether they could not cultivate some of your wonderful forms; and tempted me by saying that if they could flower them, I sh^d have plants to examine.—I said I would mention the subject to you, but that of course I doubted whether you had time and inclination to get them dug up.—They said the roots might be packed in almost dry peaty soil or charcoal in moss, and sent to “Royal Gardens[,] Kew, London,” marking what they were, i. e. terrestrial orchids from the Cape.—They ought to be dug up, when completely dormant after seeding over.—It certainly would be a treat to see a blooming *Satyrium*, or *Disperis* and the odd unnamed form! They said the safest way of all, but more troublesome, to send them, would be to plant them in pots in a box, with a [*sic*] little glazed windows on two sides under charge of some passenger. The heat starting them would be the great risk. But it is not at all likely you could spare time from your own pursuits.¹

Pray believe me, my dear Sir

Yours sincerely and obliged

CH. DARWIN

¹ Mr. Trimen informs me that a good many orchids were got together and dispatched, but (probably owing to unsuitable treatment) did not appear to prosper, and by the time a few of them contrived to flower, Darwin was too much occupied with other pressing work to be able to examine them.

3.

May¹ 23rd [1863.]

DOWN.

BROMLEY.

KENT. S.E.

MY DEAR SIR

I have delayed thanking you for your note and photograph, as I have no photograph by me of myself. I have never had a proper "carte" taken; but I enclose a photograph made of me by my son, which I daresay will do as well.—

Your accounts of the *Disa* and *Herschelia* are excellent, and your drawings first-rate. I felt so sorry that such excellent work sh'd remain locked up for an indefinite period in my portfolio, that you have made me break a solemn vow, and I have drawn up from your notes (and selected 4 figures for woodcuts) an account for Linnean Soc.—I have enlarged a little and explained and introduced a few remarks.—I hope the Soc^y will publish the paper, and if so I will send you spare copies.—The title is "On the Fertilisation of *Disa grandiflora* by Roland Trimen Esq^t of the Colon. Off. C. Town: drawn up from notes and drawings sent to C. Darwin Esq^r." ² I hope that you will approve of this, and not object to anything in the little paper.—I am very sorry to hear so poor an account of your health and that you have so little time to spare for the exercise of your

¹ The month is indistinctly written and looks more like 'July' than 'May'. Mr. Trimen had, however, noted that he received the letter at the Cape on July 20, so that this latter month cannot have been intended. Confirmation of the reading as 'May' is afforded by the presence of an envelope (two only are preserved) with the post-mark 'BROMLEY, KENT. MY 24. 63'. It also bears post-marks of 'LONDON. MY 25' and 'DEVONPORT. MY 26'. It is addressed, 'Roland Trimen, Esq, Colonial Office, Cape Town, Cape of Good Hope.'

² The paper was published in *Journ. Proc. Linn. Soc. Bot.*, vii (1863), 144.

admirable powers of observation.—I did not know all this; otherwise I sh^d not have thought of asking for plants. Think not a moment more on subject.—Indeed I *ought* to work on other subjects.—Yet I am going to ask a favour, if you know any one who dabbles in Botany, viz., for seed of any Cape *Oxalis*: several species present two forms, one with long pistil and short stamens; the other form with short pistil and longer stamens. It is of high interest to me to get seed of any such species.—To return to Orchids, I now believe that Hymenoptera and Diptera are generally the chief workers more than Lepidoptera. With respect to the limits of Rostellum; it can in most cases be told only conjecturally: in *Disa* the 2 discs (and no part of caudicle of pollinia) and the part which connects the 2 discs with the medial upward central fold or ridge, and whole *face* of column down to the two confluent stigmas, may all be considered as the rostellum or modified third stigma.—With sincere thanks and every good wish, Believe me, my dear Sir

Yours sincerely

C. DARWIN

4.

August 27th[, 1863]

DOWN.

BROMLEY.

KENT. S.E.

MY DEAR SIR

I am very much obliged for your very pleasant letter. You have hit upon the right case in *Oxalis*, and seeds will really be a treasure to me. I have posted a paper for you on the dimorphism of *Linum* which if you will read, you will see why I am anxious for *Oxalis*. I have a more curious case unpublished; but the whole class of facts strike me as very surprising. You

may rely on my statements, for they have been verified [*sic*]. *Linum perenne* agrees with your *Oxalis*. I am also very glad indeed to hear about the Peaches,—the more so as it is an exotic in S. Africa.—I am going in a weeks time to Malvern for a month to try and get a little strength, and when there I will probably draw up a notice for *Gardener's Chronicle* on your peach case.¹—

I daily expect proofs of your paper on *Disa*; a rough woodcut is made.—You must not waste time in sending me many specimens of Orchids in spirits, for I declare I do not know whether I shall ever have time to work up mass of new matter already collected on Orchids. It is capital sport to observe and a horrid bore to publish.—It pleases me to read your admiration on my beloved Orchids.—I quite agree they are intellectual beings! By the bye, I believe I have blundered in *Cypripedium*²; Asa Gray suggested that small insects

¹ Darwin had suggested in relation to fertilization by moths of Orchids which seemed to secrete no nectar, that the insects might possibly obtain palatable juices by perforating the softer tissues of some parts of the flower. Trimen informed him, as bearing on this suggestion, of two good-sized Noctuid moths (*Egybolis vaillantina*, Stoll, and *Achaea chamaeleon*, Guén.), abundant in Natal, where both were styled 'Peach Moth'—though absolutely different in appearance—because they sucked peaches (both ripe on the trees and when fallen). Trimen caught the latter in the act, and found that they had no difficulty in piercing the peach-skin with their sharp and strong haustellum. The observation is quoted by Darwin in *Fertilisation of Orchids* (1877), 40. F. Darwin later published an account of the similar behaviour of a much larger moth of the same tribe which was accounted a nuisance in Northern Australia owing to its piercing and sucking oranges! He showed how the proboscis in this moth was armed near the tip with cutting and lacerating processes.—*On the Structure of the Proboscis of Ophideres fullonica*, an orange-sucking Moth (*Quarterly Journ. of Microscopical Science*, N.S., xv. 384). The number (LX) containing the paper appeared in Oct., 1875, and it is a curious coincidence that the same organ of the same species was briefly described and well figured almost simultaneously by Künckel in the *Comptes Rendus* for Aug. 30, 1875.

² When Darwin wrote the first edition of *Fertilisation of Orchids* (1862), he misunderstood the mechanism of *Cypripedium*. In the

enter by the toe and crawl out by the lateral windows. —I put in a small bee and it did so and came out with its back smeared with pollen: I caught him and put him in again, and again he crawled out by the window: I cut open the flower and found the stigma smeared with pollen!

Read Bates *Travels* they will, I am sure, interest you. —With respect to *Physianthus*, I do not know whether fact is known; but I think it would be well worth investigating.¹ It is certain that the *Asclepiadæ* require insect aid for fertilisation. The pollen-masses are wonderfully like those of Orchids. You ought to read R. Browns admirable paper on *Asclepius* in *Transact. Linnean Soc.* about 15 or 20 years ago. In the *Apocynæ*, (which are allied to the *Asclepiadæ*) there is a genus, which catches Diptera by the hundred: I have a plant but cannot make it flourish, as I have always wished to investigate the case. It is said that the Diptera are caught by the wedge-shaped spaces between filaments of anthers. But I suspect the plant somehow profits or requires visits of insects. You ought to try whether *Physianthus* will seed if insects are excluded by a net.—I have seen Hymenoptera from N. America with numbers of pollen-masses of some *Asclepius* sticking to their tarsi;² and the pollen-masses

second edition (1877) he gives, on p. 230, Asa Gray's view, and his own observations confirming it. Mr. Francis Darwin has kindly given me these references.

¹ Darwin was here referring to a note of Trimen's about the curious manner in which Lepidoptera and many other insects are caught by a mechanical (not viscid) contrivance in the flowers of *Physianthus albens*,—a native of temperate South America. It seemed a case in which the plant *overdid* matters, the numerous visitors being nipped by hard sharp ridges closing on the proboscis when introduced into the nectaries, and the captives, in a great many cases, failed to liberate themselves and carry off the pollinia, eventually dying where they hung.

² I have myself often observed the difficulty with which insects, especially wasps and Fossors, dragged themselves free from the

are thus dragged over the stigmas.—R. Brown's paper has beautiful illustrations.—This is a disjointed, dull letter, but I have been working all day with very little strength.—

With every good wish and sincere thanks

Pray believe me

My dear Sir

Yours sincerely

CH DARWIN

5.

Nov. 25 [1863]

DOWN.

BROMLEY.

KENT, S.E.

MY DEAR SIR

I have been laid on the shelf for nearly three months, and am ordered to do nothing for 6 months by my doctors. To write this is against rules.—Many thanks for specimens of orchids and for your kind letter. I dare not look at *Oxalis* flowers. I regret much that you cannot get seed, especially of your trimorphic flowers.¹ Most species of *Oxalis* shed their seed by a spurt and the capsules are sensitive to a touch. Could you employ anyone to dig up the bulbs of the 2 or 3 forms and allow me to pay; i.e. if they are bulb-bearers.

The last job I began and broke down was a letter hold of Asclepiad flowers in North America, and how frequently their tarsi were bristling with pollen-masses. On one occasion I found a dead humble-bee held fast by the flower.

¹ In answer to Darwin's inquiries Trimen informed him that he had found trimorphic heterostyled species of *Oxalis*, and sent drawings and dried specimens. Darwin referred to this information and material in *The Different Forms of Flowers on Plants of the same Species* (1877), 169. Trimen's name is accidentally omitted from the index of this work.

to *G. Chronicle* on your Peach case.¹—I must write no more.—I live in *hopes* some day to be able to work a very little more, but it will be long before I can.—Sincere thanks for your very kind letter.

Yours very sincerely

C. DARWIN

I forwarded letter to Bates. Pray use me as often as you like.—

6.

Written by Mrs. Darwin, signed by Charles Darwin.

DOWN.

BROMLEY.

KENT. S.E.

MY DEAR MR TRIMEN

May 13. 1864

I received your letter of Mar 14, some time ago and was fearful that the *Oxalis* would never arrive, but yesterday to my joy they came safe and alive and are now planted.² Please give my sincere thanks to Mr Mac Gibbon and accept them yourself. The plants will be invaluable. My only fear is that each kind has been propagated by offsets from a single stock and if so they will all belong to the same form.

I am sorry for my mistake about the *Disa*. I have sent an erratum to *Linn. Journ.*³

Thanks for the additional facts about *Disa*, but I am sure I do not know what I shall ever do with all my wealth of new facts.

¹ See p. 224 n. 1.

² See the preceding letter (5) on p 226.

³ This was an error in Darwin's description of the position of the viscid discs of the pollinia in relation to the passages leading to the nectary; but it was partly due to the point of view from which Mr. Trimen's fig. A was taken. The position was of importance in relation to the only passages of access to the nectary where a proboscis could be pushed.

I am slowly recovering from my 10 months illness, but I do not know when I shall regain my old modicum of strength. I was pleased to see a nice little review evidently by Mr Bates on your Cape butterflies in that admirable journal *The Nat. Hist. Review*.¹

By the way do you see the "Reader". No English newspaper ever before gave half as good resumés of all branches of science: the literature is likewise well treated. I do not know who the Editor is so that my puffing is honest.

Does *Strelitzia reginæ* grow in any gardens at the Cape? I strongly suspect it must be fertilized by some honey seeking bird; the structure is very curious and this wd be worth investigating.² With cordial thanks believe me

Yours sincerely
CH. DARWIN

7.

Written by Mrs. Darwin, signed by Charles Darwin, who also inserted the words and letters printed in small capitals.

DOWN.

BROMLEY.

KENT. S.E.

MY DEAR SIR

Nov 25, 1864.

Your paper arrived quite safe. I have read it with much interest, for I have long thought the *Bonatea* one of the most curious Orchids in the world. Asa Gray

¹ Bates's very appreciative review was of Part I of Trimen's *Rhopalocera Africae Australis*, Cape Town, 1862. It appeared in *The Natural History Review* for April, 1864.

² Trimen supplied some evidence that Darwin's suspicions were well founded; for two species of Sun-bird (*Cinnyris*) frequented the flowers of *Strelitzia*. See *Cross and Self Fertilisation in the Vegetable Kingdom* (1876), 371 n.

has described in an American *Habenaria* a nearly similar contrivance with respect to the nectary as yours. I have sent your paper to *Linn. Soc.* and I hope it may be printed, but that of course I cannot say and IT may be influenced by cost of engraving.¹

With respect to the *Satyrium* I sh^d think that the pollen masses which you sent had been scraped off the head of some insect BY THE INSECT ITSELF; I do not refer to the additional pollen-masses which you saw growing *in their cases*.

Most of the *Oxalis* which you so kindly sent me flowered, but all with 2 exceptions presented one form alone. From what I know about *Primula*, I sh^d be astonished at the same bulb ever producing 2 forms. In the 2 exceptional cases, one bulb in each lot produced a distinct form; but I have very little doubt there ought to be 3 forms. I got some seed from one of the unions and have some feeble hopes that they may germinate.

If I have strength (for I keep weak) I sh^d like to make out *Oxalis*, so if you have any opportunity I should still be very glad of seed.

Many thanks about *Strelitzia*.² Would it be possible to get a plant of the kind that seeds, protected from the sugar-birds, with another plant unprotected near by?

I am tired, and so will write no more.

With many thanks pray believe me

Yours very sincerely

CH. DARWIN

¹ The paper was published in 1865. It is entitled: *On the Structure of Bonatea speciosa, Linn., with reference to its Fertilisation.*—By Roland Trimen, Memb. Ent. Soc. Lond.—*Journ. Linn. Soc.—Bot.*, ix (1865), 156. Darwin mentions this paper in his *Notes on the Fertilisation of Orchids* in *Ann. and Mag. N.H.* for September (1869), 8, 17; as also in *Fertilisation of Orchids* (1877), 76, 77.

² See p. 228

The invitation conveyed in the following letter (No. 8) exhibits the characteristic features described by Mr. Francis Darwin.¹

It was on this visit that Mr. Trimen heard Darwin speak with such strong feeling on the subject of Owen and the article in the *Edinburgh* (see p. 28 n. 2).

8.

Dec. 24th [1867]

DOWN.

BROMLEY.

KENT. S.E.

MY DEAR SIR

If you are not engaged, will you give me the great pleasure of your company here next Saturday, and stay the Sunday with us. We dine at 7 o'clock.—You would have to come by Train to Bromley, but I am sorry to say this place is six miles from the Station.

I am bound to tell you that my health is very uncertain and I am continually liable to bad days, and even on my best days I cannot talk long with anyone; but if you will put up with the best will to see as much of you as I can, I hope that you will come.—Pray believe me, My dear Sir

Yours very sincerely

CH. DARWIN

Of the remaining eleven letters six (Nos. 9–12, 15, 16) deal with subjects treated of in *The Descent of Man and Selection in relation to Sex*;²

¹ *Life and Letters*, i 139.

² The following references to information received from Roland Trimen are printed in the index of this work (Ed. 1874, 682): 'on the proportion of the sexes in South African butterflies, 250; on

a few words of encouragement on Trimen's great paper on Mimicry are contained in No. 13; the geographical distribution of beetles in No. 19. Of four brief letters, two contain invitations (Nos. 13, 14), and two are concerned with difficulties caused by ill-health (Nos. 17, 18, the latter written by Mrs. Darwin).

The first letter (No. 9) of the following series introduces, and subsequent letters return to the question of ocelli (ocellated spots or eye-spots) on the wings of butterflies and moths. It is evident, from his reference to the male peacock and inquiries as to ocelli restricted to male butterflies, that Darwin was inclined to seek an interpretation based on the hypothesis of Sexual Selection.¹ It was not known until long after the date of these letters that eye-spots together with certain differences in shape² are in the vast majority of cases characteristic of the butterfly broods of the wet season. The existing interpretation of them was first suggested by an observation made by Professor Meldola and the present writer in 1887, when a lizard was seen to exhibit special interest in an eye-spot on the wing of the English 'Small Heath' butterfly (*Coenonympha pamphilus*).

the attraction of males by the female of *Lasiocampa quercus*, 252; on *Pneumora*, 288; on difference of colour in the sexes of beetles, 294; on moths brilliantly coloured beneath, 315; on mimicry in butterflies, 325 [324]; on *Gynanisa Isis*, and on the ocellated spots of Lepidoptera, 428; on *Cyllo Leda*, 429.' Nearly all the above subjects are referred to in letters 9-12, 15, 16.

¹ Compare pp. 104, 105, 113, 125, 127, 128, 133-5, 140-1.

² Figured by Darwin in *Descent of Man*, &c. (1874), 429. See also 428 n. 48.

It examined the mark and more than once attempted to seize it. This observation has been repeated with birds and African butterflies by Mr. Guy Marshall and others, while large numbers of specimens have been collected with injuries to the wing at or near an eye-spot. Hence the conclusion that the usual value of these markings is to divert attention from the vital parts and give the insect extra chance of escape. Their disappearance from the dry season broods is interpreted as due to the paramount necessity for concealment during that time of special stress.¹

9.

Jan. 2nd [1868]

DOWN.

BROMLEY.

KENT. S.E.

MY DEAR MR TRIMEN

What you say about the ocelli [ocellated spots or eye-spots] is exactly what I want, viz the greatest range of variation within the limits of the same species,—greater than in the Meadow Brown, if that be possible. The range of difference within the same genus is of secondary interest; nevertheless if you find any good case of variation, I sh^d much like to hear how far the species of the same genus differ in the ocelli. As I know from your Orchid Drawings how skilful an artist you are, perhaps it would not give you much more trouble to sketch any variable ocelli than to describe them — I am very much obliged to you for so kindly assisting

¹ For a further account of this and other uses of these markings, together with references to the original memoirs, see 'eye-spots' in index of *Essays on Evolution* (1908), 424.

me, and for your two pieces of information in your note about the sexes of the Batchian Butterfly and about the Longicorn Beetle.—¹

With many thanks, pray believe me

Yours very sincerely

CH. DARWIN

10.

Jan. 16th[, 1868.]

DOWN.

BROMLEY.

KENT. S.E.

MY DEAR MR TRIMEN

I really do not know how to thank you enough for all the great trouble which you have taken for me.—I never saw anything so beautiful as your drawings.² I have examined them with the microscope!! When I asked for a sketch I never dreamed of your taking so great trouble.—Your letter and Proof-sheet give me exactly and fully the information which I wanted. I am very glad of the description of the ocellus in the S. African *Saturnidæ*:³ I had no idea it was so com-

¹ In *The Descent of Man* (1874), 250, Darwin quotes A. R. Wallace's observation, doubtless supplied to him by Trimen, and here referred to, that the female of *Ornithoptera croesus* was commoner and more easily caught than the male. Mr. Trimen thinks that this must be the 'Batchian Butterfly'. On p. 294 n. 63 Darwin states that he had been informed by Trimen that the male of a species of the Lamellicorn genus *Trichius* is more obscurely coloured than the female. Trimen's name is not mentioned in connexion with the similar relationship recorded for certain Longicorn beetles on pp. 294, 295.

² The drawings were illustrations of the extreme variation in the development of the eye-spots on the wings of *Cylo (Melanitis) leda*. Darwin referred to these and figured some of them in *Descent of Man* (1874), 428, 429.

³ Darwin is here evidently alluding to the description given him by Trimen of the 'S. African moth (*Gynanisa isis*), allied to our Emperor moth, in which a magnificent ocellus occupies nearly the whole surface of each hinder wing'.—*Descent of Man* (1874), 428.

plex.—If you know of any case in Lepidoptera of ocelli regularly confined to the male,¹ I sh^d much like to hear of it, as it would illustrate a little better the case of the peacock, which has often been thrown in my teeth.—I doubt whether such cases exist, and if I do not hear I will understand that you know of no such case. Again let me thank you cordially for your great kindness, and I remain,

Yours very sincerely

CH. DARWIN

11.

Written by Mrs. Darwin, signed by Charles Darwin.

DOWN.

BROMLEY.

KENT. S.E.

Feb 12 [1868.]

MY DEAR MR TRIMEN

I shall be very happy to put my name down for your brother's book and he can hand over the enclosed paper to Hardwick.²

Since you were here I have become much interested on the relative numbers of the males and females of all animals. I am particularly anxious for other cases like that from [A. R.] Wallace which you gave me of females in excess;³ or to know that such cases are rare. If you can, I am sure you will aid me.⁴ Do you give many

¹ Mr. Trimen informs me that he was unable to discover any such case.

² Mr. Trimen thinks that the book must have been the *Flora of Middlesex* (octavo, London: 1869) written and published by Henry Trimen and Sir William Thiselton-Dyer.

³ See p 233 n. 1.

⁴ This letter enclosed a slip of paper which is evidently Trimen's copy of the list sent by him in reply to Darwin's inquiry. It contains a full list of nineteen species of South African butterflies in which males are more numerous than females, and of three species

instances in your book on S. African butterflies, of males in excess. I remember writing down one or 2 cases which you gave me.

Believe me

Yours very sincerely

CH. DARWIN

12.

Feb. 21st [1868.]

DOWN.

BROMLEY.

KENT. S.E.

MY DEAR MR TRIMEN

You are always most kind in aiding me. The argument of the *Lasiocampa*¹ strikes me as very good—but what an intricate subject it is!—I have had excellent letters from Stainton and Bates. The latter is much staggered.—Have you ever heard or observed other cases like the *Lasiocampa*. I think I have seen in England many Butterflies pursuing one.—But here comes a doubt may not the same male serve more than one female. I think I will write to Dr. Wallace of Colchester.²—

in which the females are apparently the more numerous. These numbers are quoted by Darwin in *Descent of Man*, &c. (1874), 250.

¹ Mr. Trimen has kindly given me the following note:—

‘E. Blanchard (in his *Métamorphoses, Mœurs et Instincts des Insectes*) had attributed to some special and peculiar sense the power exhibited by many males among moths of discovering the distant and concealed females of their respective species. I contended that it could only be the sense of smell that was brought to bear in such cases, instancing my own experience in the case of the English ‘Oak Eggar’ (*Lasiocampa quercus*), where the males assembled to an empty box in my pocket which had contained a virgin female on the previous day.’ The observation is referred to in *Descent of Man* (1874), 252. See also Darwin’s argument in letter 15, p. 242.

² The experience of Dr. A. Wallace with the large silk-producing moths is quoted in several places in the *Descent of Man*, &c.

My women-kind have insisted on coming to London for all March, much to my grief; but I shall get some good, for I shall see some of my friends, and you amongst the number.—

With very sincere thanks

Believe me

Yours very sincerely

CH. DARWIN

I shall go doggedly on collecting facts through the animal kingdom, and possibly at the end some little light may be acquired.—I am getting some of the chief domestic animals tabulated.

In the last sentence of the following letter Darwin was referring to the evening of March 5, 1868, when Trimen read his remarkable and important paper, published in the early part of the following year: 'On some remarkable Mimetic Analogies among African Butterflies.'¹ Bates's classical paper on Mimicry (1862), referred to on pp. 122-6, was concerned with tropical American butterflies and moths. A. R. Wallace's paper 'On the Phenomena of Variation and Geographical Distribution as illustrated by the *Papilionidæ* of the Malayan Region'² (1866) dealt with the same subject as illustrated by butterflies in the tropical East. Trimen's paper completed the great series by extending the hypothesis of Mimicry to the African continent. The chief example considered in the paper, that of *Papilio dardanus* (*merope*), was by

¹ *Trans. Linn. Soc. Lond.*, xxvi. 497-522.

² *Trans. Linn. Soc. Lond.*, xxv. 1-71.

far the most complex and difficult to interpret of any in the world. When, in this masterly memoir, he had at length unravelled the tangled relationships, three 'species', up to that time regarded as entirely distinct, had been sunk as the three different mimetic females of a single non-mimetic male, then known as a fourth 'species'. Trimen's conclusions were not confirmed by the supreme test of breeding until 1902, and all three mimetic forms found in one locality were not bred from the eggs of a single parent until 1906.¹

One of the principal opponents of Trimen's conclusions was the late W. C. Hewitson, who said: 'it would require a stretch of the imagination, of which I am incapable, to believe that . . . *P. merope* . . . indulges in a whole harem of females, differing as widely from it as any other species in the genus . . .'² However, shortly after he had written the above sentence Hewitson received from one of his own collectors this very male taken paired with one of the mimetic females.³

My friend Mr. Harry Eltringham has recently pointed out to me a passage, marked by much confusion of thought, in Hewitson's *Exotic Butterflies*,⁴ which might be read as an anticipation

¹ See 'dardanus' in index of *Essays on Evolution* (1908), 414; also Plate XXIII in *Trans. Ent. Soc. Lond.* (1908), 427-45.

² *Trans. Ent. Soc. Lond.* (1874), 137.

³ *E. M. M.* (Oct., 1874), 113.

⁴ London, 1862-66, III: text of plate 'Nymphalidæ. Diadema iii.': (pages unnumbered)

of Fritz Müller's earlier suggestion that Mimicry may be due to Sexual Selection (see pp. 127-8). I do not think that the words really bear this interpretation, but even if they do, it is obvious that a suggestion intended to be taken as a joke cannot be looked upon as a serious anticipation! Inasmuch as Hewitson makes special reference to the three papers of Bates, Wallace and Trimen, it is not inappropriate to quote his criticisms at this point.

After describing some of the wonderful forms that would now be placed in the African genus *Pseudacraea* mimetic of the Acraeine genus *Platnema* from the same localities, Hewitson proceeds to remark:—

'This strange resemblance to each other of distant and very distinct groupings, which forms the romance of natural history, has afforded wonder and delight to every naturalist, and will do so to the end of time, the more so because of its mystery, unless some much better explanation is offered than that proposed by Darwin and his followers, because, unluckily for them, it is just those species which superficially bear the closest resemblance to each other that differ most in their fundamental structure.'

The objection urged by Hewitson is of course the strongest of all reasons in favour of the views he is attacking. Such fundamental differences exclude an interpretation of resemblance based simply on affinity. It is well that this important statement should be proclaimed by an opponent

of the theory of Mimicry. It is also well that he should say of the 'great leading aristocratic' groups which are resembled by other butterflies—*Danaïs*, *Acraea*, '*Heliconidae*' (including under this head *Ithomiinae* and *Danainae* as well as true *Heliconinae*¹):—

'One of the most marvellous things in this representative system is that the great groupings are not only imitated at home, but that the stragglers from two of them in other lands have their mimics as well; and in the great South American group, the *Heliconidae*, the butterflies of several genera, completely different in their neurulation, are inseparable by the unaided sight.'

It would be hardly possible to produce better indirect evidence of some special quality in the chief models than that afforded by the resemblances to them formed afresh when stragglers have wandered into other lands. Section VI of the present work is largely concerned with one striking example of the mimetic resemblance by indigenous New World species of invading *Danaines* from the Old World. Hewitson for a most singular reason rejects the conclusion that the groups in question are specially protected, and concludes by making the jocular suggestion to which Mr. Eltringham directed my attention:—

'Naturalists, Wallace, Bates, and Trimen, who have each studied one of these great groupings in their native land, tell us that they exude a liquid of an offensive

¹ See pp. 152-4.

smell. We have, however, no right to conclude that what may be unpleasant to us is not to them a sweet-smelling royal unction. May not all the imitators of these scented aristocrats be simply votaries of fashion, apeing the dress of their superiors, and, since the females take the lead, "naturally selecting" those of the gayest colours?'

Hewitson in the first part of the above paragraph assumes that the liquid is considered to be offensive *to the insects themselves*, whereas of course it is believed to protect *against insect-eating animals*. In the last part I do not think he uses the word 'naturally' when he means 'sexually', for the sake of the little play upon the former word. I think by the words 'females take the lead' Hewitson refers to the greater prevalence and perfection of female Mimicry, and that he only intended to convey the facetious suggestion of conscious and deliberate imitation.

To return to Trimen's paper, it is hardly surprising that a memoir containing such novel and startling conclusions should have been heard by a hostile audience, and my friend tells me that 'Darwin's congratulations were of immense comfort, as the large meeting was for by far the greater part opposed and discouraging'. Darwin's keen interest in Bates's paper has been shown on pp. 123-6, the part he took in encouraging Fritz Muller in his successive amendments of the Batesian Hypothesis, on pp. 126-9; but the following letter is the first evidence I

have come across of his personal interest in the immensely important contribution made by Roland Trimen.

13.

Monday
[Mar. 20, 1868]

4. CHESTER PLACE¹
REGENTS PARK
N.W.

MY DEAR MR TRIMEN

Would it suit you to come and lunch here at 1. oclock on Friday or Saturday, or indeed almost any day; or if luncheon-time does not suit you, if you will you will [*sic*] tell me at what hour you will call I will be at home.—I hear that you had a brilliant night at Linn. Soc. and I regretted so much that I could not come.

Yours very sincerely

CH. DARWIN

14.

Saturday [1868]

4 CHESTER PLACE
N.W.

MY DEAR MR TRIMEN,

Tuesday w^d suit me, but another man (Mr. Blyth²) is coming to lunch on that day, and as you know that I am not up to more than an hour's talk, I sh^d see less of you; so if equally convenient and I do not hear to contrary, I will name Wednesday at 1 oclock.

Very many thanks for your information in note.—

Yours very sincerely

C. DARWIN

¹ The house of Mrs. Darwin's sister, Miss Elizabeth Wedgwood.

² See *More Letters*, i. 62 n., for an account of this naturalist.

15.

April 14th—[1868]

DOWN.

BROMLEY.

KENT. S.E.

MY DEAR MR TRIMEN

It is very kind of you to take the trouble of making so long an extract, which I am very glad to possess, as the case is certainly a very striking one. Blanchard's argument about the males not smelling the females, because we can perceive no odour, seems to me curiously weak. It is wonderful that he sh^d not have remembered at what great distances Deer and many other animals can scent the cleanest man.¹—

Many thanks for your Photograph, and I send mine, but it is a hideous affair—merely a modified, hardly an improved, Gorilla.—

Mr [H.] Doubleday has suggested a capital scheme for estimating the number of sexes in Lepidoptera, viz by a German List, in which in many cases the sexes are differently priced.² With Butterflies, out of a list of about 300 Sp. and Vars. 114 have sexes of different prices, and in all of them, with one single exception, the male is the cheapest. On an *average* judging from price for every 100 females of each species there ought to be 143 males of the same species.—So I firmly believe that you field collectors are correct.—Nearly the same result with Moths.

¹ The 'extract' probably refers to an account of the males of the Oak Eggar moth assembling to a box that had contained the female (see p. 235 n. 1). Blanchard's argument was revived in 1894 by Prof. F. Plateau, who, finding the taste ('savour réelle') of the larva, pupa, and imago of the Magpie moth (*Abraxas grossulariata*) to be somewhat pleasant to his own palate, concluded that it was not distasteful to insectivorous animals. This conclusion is opposed by the present writer in *Trans. Ent. Soc. Lond.* (1902), 405-14.

² Quoted by Darwin in *Descent of Man*, &c. (1874), 252.

I sincerely wish you health, happiness and success in Nat. History in S. Africa. I should have much liked to have asked you, if you could have spared time, to come down here for a day or two; but Mrs. Huxley is coming here in a few days with all her six children and nurses, for healths sake, and stop some weeks. And our House will be, with others, so absolutely full, that today we have had to tell our Brother-in-law, that we cannot possibly receive him.—

Most truly do I thank you for your great kindness in aiding me in so many ways. Yesterday I was working in much of your information.—

Believe me

Yours very sincerely

C. DARWIN

16.

July 24th [1871]

DOWN,
BECKENHAM,
KENT.

MY DEAR MR TRIMEN

I am much obliged for your long and interesting letter. You asked me whether I have any notion about the meaning of moths etc flying into candles, and birds against light-houses.—I have not.—I have looked at the case as one of curiosity, which is very strong with the higher animals, and I presume even with insects. A light is a very new object, and its distance cannot be judged, but how it comes that an insect is so stupid as to go on flying into the same candle I cannot conceive. It looks as if they were drawn towards it.—Sir C. Lyell, I remember, made years ago the difficulty greater by asking me, what stops all the moths in the world flying every moon-light night up to the moon, or as near as they could get.—Perhaps they have instinctively learnt that this cannot be done.—

With respect to humour, I think dogs do have it, but it is necessarily only of a practical kind. Everyone must have seen a dog with a piece of a stick or other object in his mouth, and if his master in play tries to take it away, the dog runs with prancing steps a few yards away, squats down, facing his master, and waits till he comes *quite close* and then jumps up and repeats the operation,—looking, as if he said, “you are sold”.—

I have many letters to write so pray excuse brevity.—My book has been very successful as far as sale has been concerned, and has hitherto been in most cases treated very liberally by the press.—My notions on the moral sense have, however, been much reprobated by some and highly praised by others.—I have no news to tell, for I have seen hardly any one for months.—

I am extremely sorry to hear that you are no freer of official duties, for I feel sure if you had more leisure and especially if you lived in the country, you would make some grand new observations.—

With every good wish—

Pray believe me

Yours sincerely

CH. DARWIN

17.

*Written by Sir George Darwin, signed by
Charles Darwin.*

DOWN

BECKENHAM

MY DEAR MR. TRIMEN,

Thursd. July 27. 71

I was much surprized to receive your letter and I am sorry to hear of the cause of your hurried return to England.¹—

¹ In consequence of the death of his father in March, 1871.

I have been a good deal out of health of late and we have taken Haredene¹ for a month in order that I may get a little rest. We start tomorrow morning. I shall have very great pleasure in seeing you there after your return from Edinburgh. I am sorry to say that I cannot ask you to sleep with us as we shall have no beds to spare;—but I suppose from what you say that you will be staying in the neighbourhood. Many thanks for the Review which I will read in the course of the day.²

Believe me

Yours very sincerely

CHARLES DARWIN

18.

From Mrs. Darwin.

HAREDENE³ Tuesday

[Jul. 28–Aug. 25, 1871]

DEAR MR TRIMEN

I am very sorry to say that Mr Darwin has been so unwell (ill I may say) that we are hastening our return home as soon as possible. He is quite unequal to seeing you which he very much regrets.

Our stay in this charming place is a great disappointment, though I hope he will reap the benefit of the rest afterwards. He desires me to repeat how very sorry he is not to be able to see you

believe me

yours very truly

EMMA DARWIN

¹ Mr. Francis Darwin informs me that Haredene is near Albury in Surrey.

² Mr. Trimen thinks that the Review spoken of was a notice of the *Descent of Man*, &c., contributed by him to the *Cape Monthly Magazine* in June, 1871.

³ See the above n. 1.

19.

Nov. 13th [1871]

DOWN,
BECKENHAM, KENT.

MY DEAR MR TRIMEN

I write one line to say how sorry I am not to see you before your return to the Cape,¹ which I presume will be soon. But I cannot get my head steady enough to see anyone. I have just returned from a visit to my sister for a week, but I was forced to spend nearly all the day in my bed-room.—

I read with much interest some little time ago your paper on Geographical Distribution of Beetles; and agreed, I believe, with all your general remarks.²—

I wish you all success in your future researches and remain

Yours very sincerely
CH. DARWIN

If on the point of starting do not trouble yourself to answer this.—

¹ The letter was received Jan. 11, 1872, after Trimen had returned to the Cape.

² The paper referred to is:

Notes on the Geographical Distribution and Dispersion of Insects; chiefly in reference to a paper by Mr. Andrew Murray, F.L.S., 'on the Geographical Relations of the chief Coleopterous Fauna'—By Roland Trimen, F.L.S., &c.—*Linn. Soc. Journal.*—Zool. xii (1871), 276–84.

Murray in a very dogmatic way had in his elaborate memoir endeavoured to account for the greater part of the difficulties presented by the known existing distribution of animals and plants over the globe by the simple explanation of 'continuity of soil at some former period'. Trimen in his paper insisted on the more important methods of dispersal always at work, and traversed several of the author's statements, especially as regards oceanic islands, which had been treated by Murray as obviously surviving portions of otherwise vanished continental lands.

APPENDIX A

CHARLES DARWIN AND THE HYPOTHESIS OF MULTIPLE ORIGINS

I HAVE thought it of interest to consider in some detail Darwin's attitude towards a single one of the examples (pp. 45, 46) in which his sure judgement shines forth so conspicuously among his seniors, contemporaries and successors alike.

I select the idea that species or groups of species had arisen from 'multiple' (or 'polyphyletic') origins — a hypothesis very fashionable, during one brief period, both in America and on the Continent.

According to this hypothesis, two or more groups of animals were supposed to have arisen independently, perhaps in different countries, and subsequently by 'convergence' to have become one. The most extreme development of this view would be the incredible belief that a single species might be formed from separate bodies of individuals, arising independently from very different lines of descent, but subsequently fusing into an interbreeding community. Long before this idea became popular, it had been thought over by Darwin and seen to be worth-

less. The following references to the subject are to be found in his correspondence with Sir Joseph Hooker in 1854 and 1856, years before the publication of the *Origin* :—

1854, July 2.—‘I am glad to hear what you say about parallelism: I am an utter disbeliever of any parallelism more than mere accident.’¹

1856, July 13.—‘You say most truly about multiple creations and my notions. If any one case could be proved, I should be smashed; but as I am writing my book, I try to take as much pains as possible to give the strongest cases opposed to me, and often such conjectures as occur to me.’²

1856, July 19.—‘. . . it is absolutely necessary that I should discuss single and double creations, as a very crucial point on the general origin of species, and I must confess, with the aid of all sorts of visionary hypotheses, a very hostile one.’³

The above-quoted sentences sum up very briefly Darwin’s conclusion that evolution as he conceived of it implied that each species had appeared once only in a single continuous area and had then tended to spread from this as from a centre—implied in fact the soundness of the belief in what were then called ‘single centres of creation’. His arguments in favour of this conviction are given in great detail in the first edition of the *Origin*: first in chapter X, supporting the conclusion,—‘it is incredible that individuals identically the same should ever have been produced through natural selection from

¹ *More Letters*, i. 77.

² *More Letters*, i. 95.

³ *More Letters*, ii. 249.

parents specifically distinct'¹; secondly, in chapters XI and XII, the vast array of facts which are consistent with the belief in 'single centres of creation', and serve to explain the great apparent difficulties.

Sir Charles Lyell had also arrived at the firm conviction that species had spread from single centres, and, within a few days of Darwin's expression of the same conviction in July, 1856, he also was writing to Hooker and telling of his unnecessary fears:—

1856, July 25.—'I fear much that if Darwin argues that species are phantoms, he will also have to admit that single centres of dispersion are phantoms also, and that would deprive me of much of the value which I ascribe to the present provinces of animals and plants, as illustrating modern and tertiary changes in physical geography.'²

It is clear that Darwin heard of Lyell's apprehensions and was referring to them in the two following passages in letters to Hooker:—

1856, July 30.—'I cannot conceive why Lyell thinks such notions as mine or of 'Vestiges' will invalidate specific centres.'³

1856, Aug. 5.—'I suppose, in regard to specific centres, we are at cross purposes; I should call the kitchen garden in which the red cabbage was produced, or the farm in which Bakewell made the Shorthorn cattle, the specific centre of these *species*! And surely this is centralisation enough!'⁴

When, however, the *Origin* had appeared, and Lyell was for a time resisting its appeal, he

¹ *Origin of Species* (1859), 352.

² *Life and Letters*, II. 83. Quoted from *Life of Sir Charles Lyell*, II. 216.

³ *Ibid.*, 81.

⁴ *Ibid.*, 82.

was not unwilling to contemplate multiple centres with a vengeance; for he put forward as a difficulty the fact that mammals had not arisen independently on oceanic islands. Referring to this point, Darwin wrote to him (September 1, 1860) as follows:—

‘With respect to a mammal not being developed on any island, besides want of time for so prodigious a development, there must have arrived on the island the necessary and peculiar progenitor, having a character like the embryo of a mammal; and not an *already developed* reptile, bird or fish. We might give to a bird the habits of a mammal, but inheritance would retain almost for eternity some of the bird-like structure, and prevent a new creature ranking as a true mammal.’¹

Lyell does not appear to have been convinced by the argument, and Darwin wrote again on September 23, 1860:

‘I have a very decided opinion that all mammals must have descended from a *single* parent [species]. Reflect on the multitude of details, very many of them of extremely little importance to their habits (as the number of bones of the head, &c., covering of hair, identical embryological development, &c. &c). Now this large amount of similarity I must look at as certainly due to inheritance from a common stock. I am aware that some cases occur in which a similar or nearly similar organ has been acquired by independent acts of natural selection. But in most of such cases of these apparently so closely similar organs, some important homological difference may be detected.’²

Lyell had argued that, just as man would now keep down any new man that might be developed, so the bats and rodents of oceanic islands may

¹ *Life and Letters*, ii. 335.

² l c., ii. 341.

have prevented the independent origin of other mammals. To this argument Darwin replied :

‘I know of no rodents on oceanic islands (except my Galapagos mouse, which *may* have been introduced by man) keeping down the development of other classes. Still *much* more weight I should attribute to there being now, neither in islands nor elsewhere, [any] known animals of a grade of organisation intermediate between mammals, fish, reptiles, &c., whence a new mammal could be developed. If every vertebrate were destroyed throughout the world, except our *now well-established* reptiles, millions of ages might elapse before reptiles could become highly developed on a scale equal to mammals; and, on the principle of inheritance, they would make some quite *new class*, and not mammals; though *possibly* more intellectual!’¹

Many years later, in a letter to the Duke of Argyll (September 23, 1878), Darwin gave a more complete answer to the extreme supporters of the hypothesis of multiple origins, at the same time refuting the opinion—not uncommon even at the present day—that a terrestrial species such as man may exist on Mars or on some other body outside the earth. For Darwin shows in the following letter that, in order to produce the same species twice over, the same material must have been subject to the same selection at every stage, right back to the unknown starting-point of organic evolution.

‘As far as I can judge, the improbability is extreme that the same well-characterised species should be produced in two distinct countries, or at two distinct times. It is certain that the same variation may arise in two distinct places, as with albinism or with the nectarine on peach-trees.

¹ Sept. 23, 1860. *Life and Letters*, ii. 344.

But the evidence seems to me overwhelming that a well-marked species is the product, not of a single or of a few variations, but of a long series of modifications, each modification resulting chiefly from adaptation to infinitely complex conditions (including the inhabitants of the same country), with more or less inheritance of all the preceding modifications. Moreover, as variability depends more on the nature of the organism than on that of the environment, the variations will tend to differ at each successive stage of descent. Now it seems to me improbable in the highest degree that a species should ever have been exposed in two places to infinitely complex relations of exactly the same nature during a long series of modifications. An illustration will perhaps make what I have said clearer, though it applies only to the less important factors of inheritance and variability, and not to adaptation—viz., the improbability of two men being born in two countries identical in body and mind. If, however, it be assumed that a species at each successive stage of its modification was surrounded in two distinct countries or times, by exactly the same assemblage of plants and animals, and by the same physical conditions, then I can see no theoretical difficulty [in] such a species giving birth to the new form in the two countries.’¹

The Duke misunderstood the letter, for he used it as evidence to support his assertion ‘that Charles Darwin assumed mankind to have arisen at one place, and therefore in a single pair’. It is obvious that no such conclusion follows from Darwin’s argument; but in order to settle the question once for all, Sir William Thiselton-Dyer published a letter² in which Darwin makes the following statement :

¹ *Nature*, xliii. 415. At the conclusion of the letter Darwin refers his correspondent to p. 100 of the sixth ed. of the *Origin*. See also *More Letters*, i. 377, 378.

² *Nature*, xliii. 535. See also *More Letters*, i. 378–81.

‘I dispute whether a new race or species is necessarily, or even generally, descended from a single or pair of parents. The whole body of individuals, I believe, become altered together—like our race-horses, and like all domestic breeds which are changed through “unconscious selection” by man.’

This passage was written (Nov. 25, 1869) in a letter to G. Bentham as a criticism of the following passage in his presidential address to the Linnean Society on May 24, 1869:

‘We must also admit that every race has probably been the offspring of one parent or pair of parents, and consequently originated in one spot.’

The Duke of Argyll had inverted Bentham’s proposition, as pointed out by Sir W. Thiselton-Dyer.

On this remarkable page in the history of thought we see how Darwin, by sure and penetrating genius, rises to heights far beyond those attained by the men of his own and later days. We see Lyell in fear and doubt lest his cherished belief in ‘single centres of creation’ should be endangered by the one man who held the same belief on much stronger grounds. We find the great geologist, at a later stage, ready to give up his belief if he can thereby obtain a weapon against evolution; and observe, in Darwin’s answer to him and to the Duke of Argyll, an entire grasp of the problem conspicuously wanting in those authorities who expressed, at a later date, an ill-founded enthusiasm for the worthless hypothesis of multiple origins.

APPENDIX B

DARWIN AND EVOLUTION BY MUTATION

I HAVE spoken on pages 43 and 44 of the frequency with which Darwin, between 1860 and 1880, was brought back by others to a motive cause of evolution based on 'sudden jumps', or 'monstrosities', on 'large', 'extreme', and 'great and sudden' variations. Such views were continually urged upon him by 'his correspondents, and by reviews and criticisms of his work'. It is I think of interest, in relation to the biological fashions of the day, to show by many examples how firmly he met such suggestions whenever they were made to him. I therefore append the following quotations from his letters to those on pages 43 and 44 and to be found in the *Quarterly Review*¹:

(1) 1860. '... he [Harvey] assumes the permanence of monsters, whereas, monsters are generally sterile, and not often inheritable.'²

(2) 1860. 'It would take a good deal more evidence to make me admit that forms have often changed by *saltum*.'³

(3) 1860. 'Although I fully agree that no definition can be drawn between monstrosities and slight variations (such as my theory requires), yet I suspect there is some distinction. Some facts lead me to think that monstrosities supervene generally at an early age; and after attending to the subject I have great doubts whether species in a state of nature ever become modified by such sudden jumps as would result from the Natural Selection of monstrosities.'⁴

¹ July, 1909; 10-12, 25, 26.

² To Sir Charles Lyell, Feb. 18, 1860.—*Life and Letters*, ii. 275.

³ To Sir Joseph Hooker, Feb., 1860.—*Ibid.*, 274.

⁴ To Maxwell Masters, April 13, 1860.—*More Letters*, i. 147, 148.

(4) 1860. 'About sudden jumps: I have no objection to them—they would aid me in some cases. All I can say is, that I went into the subject, and found no evidence to make me believe in jumps; and a good deal pointing in the other direction.'¹

(5) 1871. '... I have now almost finished a new edition of the *Origin*, which Victor Carus is translating. There is not much new in it, except one chapter in which I have answered, I hope satisfactorily, Mr. Mivart's supposed difficulty on the incipient development of useful structures. I have also given my reasons for quite disbelieving in great and sudden modifications.'²

(6) 1873. 'It is very difficult or impossible to define what is meant by a large variation. Such graduate into monstrosities or generally injurious variations. I do not myself believe that these are often or ever taken advantage of under nature. It is a common occurrence that abrupt and considerable variations are transmitted in an unaltered state, or not at all transmitted, to the offspring, or to some of them. So it is with tailless or hornless animals, and with sudden and great changes of colour in flowers.'³

(7) 1880. 'It is impossible to urge too often that the selection from a single varying individual or of a single varying organ will not suffice.'⁴

(8) 1880. Finally the letter to *Nature*, dated November 5, 1880, was one of the strongest things ever written by Darwin. It originally contained a passage which the writer omitted on the advice of his most combative friend Huxley. The two grounds on which Darwin based his emphatic protest are stated in the following passage. A mutationist conception of evolution based on 'extreme variation' is the

¹ To W. H. Harvey, August, 1860.—*More Letters*, i. 166.

² To E. Hückel, December 27, 1871.—*More Letters*, i. 335.

³ To R. Meldola, August 13, 1873.—*More Letters*, i. 350.

⁴ To A. R. Wallace, January 5, 1880.—*More Letters*, i. 384.

first of them ; the assumption that he had made Natural Selection the sole motive cause of evolution forms the second :

‘I am sorry to find that Sir Wyville Thomson does not understand the principle of Natural Selection, as explained by Mr. Wallace and myself. If he had done so, he could not have written the following sentence in the Introduction to the Voyage of the *Challenger*: “The character of the abyssal fauna refuses to give the least support to the theory which refers the evolution of species to extreme variation guided only by Natural Selection.”’¹

APPENDIX C

WORK ESSENTIAL FOR DARWIN'S HEALTH AND COMFORT

THE alteration in tastes and interests which Darwin described in himself has been wrongly interpreted. The errors have been widely spread and are repeated by able and influential writers even at the present day.² It is important in justice to scientific men as a body and especially to Darwin himself to show by repeated evidence the true cause of the changes set down in the autobiography. I have therefore added a number of quotations from Darwin's letters to the evidence brought forward on pages 59-66 and yielded by the correspondence with Roland Trimen on pages 218 to 246. The two passages written in 1859 refer to the preparation of the *Origin of Species* :—

¹ *More Letters*, i. 388. See *Nature*, Nov 11, 1880, p. 32

² See pp. 79-83.

1859. 'I have been so poorly, the last three days, that I sometimes doubt whether I shall ever get my little volume done, though so nearly completed . . .'¹

1859. '. . . I can truly say I am *never* idle; indeed, I work too hard for my much weakened health; yet I can do only three hours of work daily, and I cannot at all see when I shall have finished.'²

1864. 'I honour your wisdom at giving up at present Society for Science. But, on the other hand, I feel it in myself possible to get to care too much for Natural Science and too little for other things.'³

1865. 'What a wonderful deal you read; it is a horrid evil for me that I can read hardly anything, for it makes my head almost immediately begin to sing violently. My good womenkind read to me a great deal, but I dare not ask for much science, and am not sure that I could stand it.'⁴

1868. 'It is really a great evil that from habit I have pleasure in hardly anything except Natural History, for nothing else makes me forget my ever-recurrent uncomfortable sensations.'⁵

1868. The concluding sentences of the following passage are quoted on pages 64 and 65, but it is of interest to print them again together with the words that led up to them. The passage first graphically describes the changes in Darwin's mind, and then clearly explains and interprets what has been so often and so injuriously misunderstood.⁶

'I am glad you were at the 'Messiah', it is the one thing that I should like to hear again, but I dare say I

¹ To J. D. Hooker: March 5.—*Life and Letters*, ii. 149.

² To Asa Gray, Apr. 4.—*Life and Letters*, ii. 155.

³ To T. H. Huxley, April 11.—*More Letters*, i. 247.

⁴ To J. D. Hooker, Sept. 27.—*Life and Letters*, iii. 40.

⁵ To J. D. Hooker, Feb. 3.—*Life and Letters*, iii. 75.

⁶ See especially pp. 79–83.

should find my soul too dried up to appreciate it as in old days; and then I should feel very flat, for it is a horrid bore to feel as I constantly do, that I am a withered leaf for every subject except Science. It sometimes makes me hate Science, though God knows I ought to be thankful for such a perennial interest, which makes me forget for some hours every day my accursed stomach.'¹

1869. 'I have been as yet in a very poor way; it seems as soon as the stimulus of mental work stops, my whole strength gives way.'²

1876. '--and then home to work, which is my sole pleasure in life.'³

1878. 'Thank Heaven, we return home on Thursday, and I shall be able to go on with my humdrum work, and that makes me forget my daily discomfort.'⁴

APPENDIX D

DE VRIES'S 'FLUCTUATIONS' HEREDITARY ACCORDING TO DE VRIES, NON-TRANSMISSIBLE ACCORDING TO BATESON AND PUNNETT

SINCE the note on p. 49 was written I have had the opportunity of reading the whole of the Presidential Address to the Zoological Section at Winnipeg, a copy having been kindly sent to me by my friend Dr. Shipley. I find that the account of fluctuations which is so diametrically opposed to that given by the author of this term in its technical sense, is adopted from Mr. R. C. Punnett's little work *Mendelism* (2nd edit., Cambridge, 1907), a fact omitted from the necessarily abridged

¹ To J. D. Hooker, June 17.—*Life and Letters*, iii. 92.

² To J. D. Hooker, June 22.—*Life and Letters*, iii. 106.

³ To G. J. Romanes, May 29.—*More Letters*, i. 364.

⁴ To G. J. Romanes, Aug. 20.—*More Letters*, ii. 48.

report in the *Times*. While Dr. Shipley's words, quoted on p. 49, are perhaps a little more precise than those of Mr. Punnett,¹ Professor Bateson's statement is more definite still:—

'For the first time he [de Vries] pointed out the clear distinction between the impermanent and non-transmissible variations which he speaks of as *fluctuations*, and the permanent and transmissible variations which he calls *mutations*.'²

Professor Bateson and Mr. Punnett are the chief exponents of de Vries in this country. It may be assumed, I think, that de Vries reaches the British public through the 85 pages of Mr. Punnett's booklet rather than through the 847 pages of the only volume by the Dutch botanist which has until now appeared in the English language.³ The unfortunate misrepresentation of de Vries is therefore certain to have led, and, in spite of this correction, is still, I fear, certain to lead, to utter confusion of thought in a subject only too likely to become obscure without adventitious assistance.

The extent of this unintentional, but very serious, misrepresentation of an authority by his exponent, can be most clearly shown by printing together passages by de Vries and Bateson from

¹ 'Of the inheritance of mutations there is no doubt. Of the transmission of fluctuations there is no very strong evidence. It is therefore reasonable to regard the mutation as the main, if not the only, basis of evolution.' (p. 72.)

² *Mendel's Principles of Heredity*, Cambridge (1909), 287.

³ *Species and Varieties: their Origin by Mutation*. Chicago and London. Second edit., 1906.

the same volume—*Darwin and Modern Science* (Cambridge, 1909). The following passage on pp. 83 and 84 is written by de Vries :—

‘ Thus we see that the theory of the origin of species by means of natural selection is quite independent of the question, how the variations to be selected arise. They may arise slowly, from simple fluctuations, or suddenly, by mutations; *in both cases natural selection will take hold of them, will multiply them if they are beneficial, and in the course of time accumulate them, so as to produce that great diversity of organic life, which we so highly admire.*’

On p. 95, only eleven pages further on, we find the following statement made by Professor Bateson, a statement which entirely contradicts the words I have italicized in the quotation from de Vries :—

‘ First we must, as de Vries has shown, distinguish real, genetic, variation from *fluctuational* variations, due to environmental and other accidents, which cannot be transmitted.’

I freely grant that de Vries’s statement, taken as a whole, does not appear to be very consistent with much that he has written.¹ He is stating alternative views as to the origin of selected variations, but the italicized words could never have been written by one who did not maintain the hereditary transmission of fluctuations; and this belief is, as will be shown below, implied in many another passage, to be found with sufficient labour in de Vries’s voluminous and somewhat obscurely written treatises.

¹ See also *Quarterly Review* (July, 1909), 30.

In a striking metaphor Professor Bateson has objected to the use of the term 'variation' to express certain different forms presented by the individuals of a species: 'We might as well,' he says with a fine scorn, 'use one term to denote the differences between a bar of silver, a stick of lunar caustic, a shilling, or a teaspoon.'¹ It would indeed be unreasonable thus to denote the *differences* between those objects, although their *agreement* may be quite properly expressed by the single phrase 'forms of silver'. 'Variation,' too, may be reasonably used in a generic sense to cover many widely different departures from what is regarded as the normal form of a species. But, to make use of Professor Bateson's metaphor, we are now threatened with the sort of confusion that would arise if (1) A declared that the word 'teaspoon' meant a teaspoon, and (2) B and C spread broadcast the statement that A had really applied this term not to a teaspoon at all, but to a shilling.

It is probable that Professor Bateson's and Mr. Punnett's error arose when they became aware that de Vries attributed 'fluctuations' to nutrition, using this term in a broad sense. They do not appear to have realized that, whereas regression rendered evident through heredity is the essential element in de Vries's 'fluctuations', the opinion that they are acquired is quite unessential. De Vries, in fact, treats the trans-

¹ *Report Brit. Assoc.*, Cambr. (1904), 576.

mission of acquired characters with a levity justly rebuked by Mr. R. H. Lock in the following passage :—

‘ . . . de Vries believes that individual variability depends entirely upon nutrition ; but under this head he includes practically the whole environment of plants—light, space, soil, moisture, and the like. Characters acquired in a similar way by previous generations are inherited, and the effect of conditions upon the developing seed whilst still borne upon the parent plant may be considerable. Thus easily does de Vries dispose of the puzzling question of the inheritance or non-inheritance of acquired characters. Acquired characters are inherited ; they are not of any importance in the origin of species.’¹

It will now be well to show from several passages that de Vries considers ‘fluctuations’ to be hereditary, and that the limits which he assigns to them only become manifest by means of heredity.

‘ . . . we must,’ says Mr. Punnett, ‘recognise with de Vries the type of variation which he has termed fluctuating.’² In order to ensure an accurate recognition it will be safest to quote de Vries’s words.

(1) In the celebrated *Mutationstheorie* (Leipzig, 1901, I.) de Vries states that, in advocating the use of the term ‘fluctuation’, he is merely adopting a word often used by Darwin himself. Thus,

¹ *Variation, Heredity and Evolution*, London, 1909, 2nd Ed., 155. See also passage (1) quoted from Mr. Lock on p. 270.

² *Mendelism*, R. C. Punnett, 2nd Ed., Cambr. (1907), 70.

³ An example of Darwin’s use of the words ‘fluctuating variability’ is to be found in the following passage from a deeply interesting

speaking of 'individual variability', he says on pages 36 and 37: 'This [form of] variability has been termed, *fluctuating, gradual, continued, reversible, limited, statistical, and individual*. The latter designation appears to be most widely spread in the domain of zoology and anthropology, whilst the term fluctuating or flowing which was frequently used by Darwin, ought certainly to be the best.' That regression, only evident through heredity, is characteristic of fluctuations, is stated on p. 38: 'Individual variability is, by propagation [literally by sowing], revertent into itself.' Again, on pages 38 and 39:—

'Auf dem Gebiete der individuellen Variabilität führt die Selection zu der Entstehung der Rassen. Dabei ist aber, wie wir bereits gesehen haben, dieses letztere Wort in einem anderen Sinne gebräuchlich, als in der Anthropologie.' Die principielle Differenz dieser sogenannten veredelten Rasse einerseits mit Varietäten, Unterarten, elementaren

letter, criticizing the hypothesis of the direct influence of environment as a motive cause of evolution:—

'In regard to thorns and spines I suppose that stunted and [illegible] hardened processes were primarily left by the abortion of various appendages, but I must believe that their extreme sharpness and hardness is the result of fluctuating variability and the "survival of the fittest".' In a letter to G. H. Lewes, Aug. 7, 1868. *More Letters*, i. 308.

¹ De Vries is here referring to p. 29, where he distinguishes the two kinds of races as follows. It will be seen that the hereditary transmission of fluctuations selected by the breeder is even more clearly expressed than in the passage quoted in the text:—

'Aber das Wort Rassen hat bekanntlich eine doppelte Bedeutung. Es bedeutet sowohl die durch Selection veredelten Rassen unserer Züchter, als auch die vorhandenen, constanten Unterarten unbekannter Abstammung.'

['But the word races has, as we all know, a double meaning. It signifies races improved by the selection of our breeders as well as existing, constant sub-species of unknown origin.']

Arten, *incipient species* u. s. w. andererseits, soll den Gegenstand unseres dritten Kapitels bilden.'

['Within the domain of individual variability selection leads to the origin of races, but, in considering this question, as we have already seen, this latter word [races] is used in a different sense to that employed in Anthropology. The essential characteristics of this so-called improved race, on the one hand, and of, on the other hand, varieties, sub-species, elementary species, *incipient species*, &c., &c., will constitute the subject-matter of my third chapter.']

I would ask how it is possible for races to arise or to be improved by the selection of individual variations (or fluctuations) if it be supposed that those latter are non-transmissible by heredity.

The German of the latter part of the passage quoted on pp. 263-4 is not very clearly expressed. My friends who are experienced in the rendering of German into English have generally found themselves puzzled by it, at any rate on a first reading. Professor A. A. Macdonell tells me that the obscurity is due to the use of 'mit' for 'und der'. At the same time he is sure that the 'einerseits' and 'andererseits' express a contrast which is unintentionally softened down by the use of 'mit'. This conclusion, based on purely linguistic grounds, is confirmed by a consideration of the subject-matter; for every student of de Vries knows that all the forms in the category beginning 'Varietäten' are explained by him as 'mutations', and are as a matter of fact in many parts of his works sharply contrasted with the products derived by selection from 'fluctuations'.

I have considered these passages in some detail because Dr. Shipley informs me that the interpretation of de Vries's 'fluctuations' as non-transmissible by heredity is based upon this portion of the first volume of the *Mutationstheorie*.

(2) Speaking of the means by which the individual steps of evolution are brought about, de Vries says:—

'On this point Darwin has recognized two possibilities. One means of change lies in the sudden and spontaneous production of new forms from the old stock. The other method is the gradual accumulation of those always present and ever fluctuating variations which are indicated by the common assertion that no two individuals of a given race are exactly alike. The first changes are what we now call "mutations", the second are designated as "individual variations", or as this term is often used in another sense, as "fluctuations". Darwin recognized both lines of evolution; Wallace disregarded the sudden changes and proposed fluctuations as the exclusive factor.'

It has been abundantly shown in the present volume (pp. 43, 44, 254-6) that de Vries is wholly mistaken in ascribing to Darwin a belief in evolution by mutation, and in maintaining that there was in this respect any difference between the two discoverers of Natural Selection. It is amusing to observe the reason given by de Vries for preferring the term 'fluctuation'. May we hope that he will abandon the word now that it too 'is often used in another sense'?

¹ Hugo de Vries, *Species and Varieties: their Origin by Mutation* Second Ed., Chicago and London (1906), 7, 8.

Fluctuations are, according to de Vries, unable, however rigidly and however long selected, to lead to progressive evolution. The following passages in which this belief is expressed, assert perfectly clearly that these limitations—rashly assumed to be permanent—are revealed by means of heredity. They also plainly show that de Vries, in maintaining the uselessness of ‘fluctuations’ as the material for progressive evolution, is merely availing himself of a principle established much earlier and on far firmer grounds by Francis Galton—the well-known principle of ‘recession towards mediocrity’ :—

(3) ‘Fluctuations always oscillate round an average, and if removed from this for some time, they show a tendency to return to it. This tendency, called retrogression, has never been observed to fail, as it should, in order to free the new strain from the links with the average, while new species and new varieties are seen to be quite free from their ancestors and not linked to them by intermediates.’¹

In the following passage, as well as in (5), de Vries is of course referring to ‘fluctuations’ :—

(4) ‘. . . Long-continued selection has absolutely no appreciable effect. Of course I do not deny the splendid results of selection during the first few years, nor the necessity of continued selection to keep the improved races to the height of their ameliorated qualities. I only wish to state that the work of selection here finds its limit and that centuries and perhaps geologic periods of continued effort in the same direction are not capable of adding anything more to the initial effect.’²

¹ *Species and Varieties*, 18.

Ibid., 790-1.

After reading the impetuous conclusions expressed at the end of the last-quoted passage, it is refreshing to turn to Darwin's calm and convincing statement in the letter quoted on p. 48.

(5) 'Even sugar-beets, the oldest "selected" agricultural plants are far from having freed themselves from the necessity of continuous improvement. Without this they would not remain constant, but would retrograde with great rapidity.'¹

It will now be of interest to inquire how de Vries's 'fluctuations' have been understood by others, and especially by his friend and fellow countryman, Professor A. A. W. Hubrecht, the distinguished zoologist. A few years ago Professor Hubrecht wrote an account of de Vries's contributions to evolutionary thought in the *Popular Science Monthly*.² The editor has added the following note to the article (p. 205): 'This article was written in English by Professor Hubrecht, the eminent Dutch zoologist, who has an equal command of the French and German languages.' Every one who has the privilege of the friendship of Professor Hubrecht and knows of his great linguistic powers will agree that probably no other man is so qualified to express de Vries's precise meaning in the English language. I select seven passages from the article in question. All of them would be meaningless if 'fluctuations' are supposed to be non-transmissible by heredity.

¹ *Species and Varieties*, 109

² For July, 1904: 205-23, 'Hugo de Vries's Theory of Mutations.'

(1) 'The different degrees of fluctuating variability can undoubtedly be seized upon by any one who wishes to make them the starting-point for the breeding of certain distinct variations. Thus, for instance, by constantly selecting for the reproductive process those plants in which a given deviation is strongly marked, after a certain time and after a series of generations, a plant can be obtained for which the Galton curve would indicate a displacement of its culminating point in the direction of the selected variation. In this way an increase in the yield of sugar obtained from the beet roots has been arrived at from about 7 per cent. to 13 or 14 per cent. Thus also ears of maize have been produced that bore 20 rows of grain, whereas the kind from which the experiment had started always bore 12 to 14 rows.

'As soon, however, as such conscious and voluntary selection ceases, the next generations successively return to the original curve.' (p. 209.)

(2) '. . . breeding variations to the right or to the left of the norm, can never exceed certain limits. Agencies are at work there which prevent the fluctuating variability from going any further. The existence of such limits compels us to acknowledge that there is no possibility that species might arise in nature according to the same plan by which certain breeds originate under artificial selection.' (pp. 209-10).

(3) 'We have seen that fluctuating variability leads to slow changes and furnishes farmers with the material to improve the races of animals and plants.' (p. 210.)

(4) '. . . by means of fluctuating variability certain local and improved races may indeed be bred, but that in nature new species never arise through its agency.' (p. 210.)

(5) 'As long as the mutation has not appeared, there can be no question of the origin of a new species; the species is then constant, and only submitted to fluctuating variability, which can produce local races (not elementary species) under the constant cooperation (either artificial or natural) of selection, but which never leads to the formation of species.' (p. 216.)

(6) 'The elementary species are stable. Selection calls

forth different races within the limits of these species, but whenever selection ceases the race is turned back to the parent form. The maximum deviation in these races is generally obtained after three or four generations of continuous selection; it takes about as many generations to bring back the parent form.' (p. 219.)

(7) 'The fact that artificial selection of fluctuating varieties, as well as hybridizing, etc., has already led to such indisputable improvements in the different races of animals and plants may, however, etc.' (p. 223.)

Finally in an article only published about a year ago in the *Contemporary Review*¹ Professor Hubrecht says :—

'Wherever our agriculturist succeeds by the most careful artificial selection in producing (*e. g.*) a beetroot of which the percentage of sugar has been raised, say, to 15 per cent. out of roots which originally stood at 7 to 8 per cent., he knows that the fluctuating variation of the beetroot has permitted him to attain this end; but he knows, at the same time, that what he has obtained is not a new species of beetroot, richer in sugar, but a product of nature which the moment it is left to itself and freed from the bonds of artificial selection goes back to an inferior sugar-producing root again.' (p. 633.)

I will now prove, although more briefly, that other writers have understood de Vries correctly. The sectional heading employed by Professor C. B. Davenport—'MUTATION vs. SUMMATION OF FLUCTUATIONS'²—is sufficient to show this; for summation would be impossible without hereditary transmission. We do not, however,

¹ For Nov., 1908, 'Darwinism versus Wallaceism.'

² *Fifty Years of Darwinism*, New York (1909), 173.

need to base our proofs upon inference, for Prof. Davenport makes the following clear statement :—

‘Does the breeder actually introduce new characters into the organic world by summing fluctuations? De Vries insists that the improvement that follows selection nearly or wholly ceases after four or five generations, and if selection be abandoned the race rapidly returns to its primitive condition.’¹

The two following passages are quoted from Mr. R. H. Lock’s book² :—

(1) ‘There are some, including de Vries, who regard all fluctuating variations (individual differences) as being of the nature of acquired characters, and as being at the same time capable of hereditary transmission, although de Vries believes the amount of progress possible in this way to be strictly limited.’ (p. 75; see also the passage quoted from Mr. Lock on p. 262.)

(2) ‘The actual effect of this kind of selection is well illustrated by the results of the processes employed in the sugar-beet industry, in which elaborate care is taken to select those roots which contain the highest percentage of sugar for the purpose of propagation. This process was followed at first by a rapid improvement, but the rate at which the percentage of sugar increased soon fell off, until at the present day all that selection can effect is to keep up the standard of excellence already attained.

‘There is no reason to doubt that a thoroughly efficient method of selection would have worked its full effect in a few generations.

‘From his own experiments, de Vries has come to the conclusion that, when selection is really efficient, the full possible effect of this process is exhausted in quite a small

¹ *Fifty Years of Darwinism*, New York (1909), 173–4.

² *Variation, Heredity and Evolution*. London, 1909. Second Ed.

number of generations, and that then the only further effect of selection is to keep up the standard already arrived at.' (pp. 135-6.)

Professor J. Arthur Thomson¹ in the first of the following passages clearly states the germinal origin of fluctuations, in the second correctly expresses de Vries's conclusions:—

(1) '... when we collect a large number of specimens of the same age from the same place at the same time, we often find that no two are exactly alike. They have peculiarities of germinal origin—or, in other words, they show *individual or fluctuating variations*.' (p. 78.)

(2) 'Fluctuations do not lead to a permanent change in the mean of the species unless there be a very rigorous selection, and even then, if the selection be slackened, there is regression to the old mean: mutations lead *per saltum* to a new specific position, and there is no regression to the old mean.' (p. 98.)

I have brought perhaps unnecessarily ample evidence in support of the fact that de Vries's 'fluctuations' are assumed by him to be transmissible by heredity, and that this assumption is an essential element in the author's definition of his technical term. When we remember that they are just the 'individual differences' of Darwin, and that de Vries's belief in their powerlessness for continued evolution is based on Francis Galton's well-known law of recession, it is really waste of time to inquire whether they are transmissible. But such positive statements to the contrary have been made by the most prominent

¹ *Heredity*, London, 1908.

supporter of de Vries in this country—statements accepted and widely circulated by others—that it appeared expedient to produce even redundant proof that the Dutch botanist has been unintentionally but fundamentally misrepresented in a matter of supreme importance.

In conclusion I think it may be convenient to sum up briefly a few opinions that have been expressed during the past fifty years as to the variations which form the steps of evolutionary progress. Such a short statement, which I will endeavour to express as clearly as possible, may do something to bring within reasonable limits those unduly exaggerated estimates of recent achievement which tend in the long run to diminish rather than to exalt the fame of an investigator.

CHARLES DARWIN. It has been shown on many pages of this book that Darwin recognized *large variations* transitional into *individual differences*, but that, with A. R. Wallace, he believed the onward steps of evolution were supplied by the latter and not by the former.¹ He admitted that advance might be arrested by

¹ The following passage is quoted from p 45 of the 1st Edition of the *Origin*:—‘Again, we have many slight differences which may be called individual differences, such as are known frequently to appear in the offspring from the same parents, or which may be presumed to have thus arisen, . . .’ ‘These individual differences are highly important for us, as they afford materials for natural selection to accumulate, in the same manner as man can accumulate in any given direction individual differences in his domesticated productions’

the limits of variation, but did not believe that the limits were necessarily permanent. He held that *the appearance of variations* was an indirect response to the conditions of life, their *character* being determined by internal causes and not by the nature of the external stimulus.

It is generally assumed that Darwin did not consider the question of the hereditary transmission of acquired characters. Professor Meldola has, however, pointed out to me the following interesting passage which has appeared, with only the slightest verbal change, in all editions of the *Origin* :—

‘Some authors use the term “variation” in a technical sense, as implying a modification directly due to the physical conditions of life; and “variations” in this sense are supposed not to be inherited: but who can say that the dwarfed condition of shells in the brackish waters of the Baltic, or dwarfed plants on Alpine summits, or the thicker fur of an animal from far northwards, would not in some cases be inherited for at least some few generations? and in this case I presume that the form would be called a variety’ (1st Ed., 44, 45).

Mr. Francis Darwin can throw no light upon the ‘authors’ referred to. It is deeply interesting to observe that Darwin did not, even in 1844, believe in the inheritance of the effects of mutilation or of mechanical pressure.¹

FRANCIS GALTON investigated the hereditary transmission of individual differences and proved

¹ *The Foundations of the Origin of Species*, Cambridge (1909), 60-1.

that many are subject to the law of 'recession towards mediocrity'. He considered that evolution proceeds by the selection of large variations (saltation) as well as of small. He suggested that certain variations do not obey the law of recession, but are the expression of a sudden leap to a new position of genetic stability. He thus anticipated de Vries in both 'Fluctuations' and 'Mutations', proposing for the latter type of variation the far better and far more descriptive term 'transilient'.

The conclusion that evolution has been 'discontinuous', proceeding by means of relatively large steps, was urged with much vigour by Professor Bateson in his work *On Variation* (1894). It was in a review of this book that Galton proposed the term 'transilient', although the opinion that evolution may take place by large steps had been expressed by him at a much earlier date.

AUGUST WEISMANN revealed the unsubstantial nature of the evidence on which the hereditary transmission of acquired characters¹ was believed.

¹ It may be convenient to quote three passages from the author's *Essays on Evolution* (1908):—

(1) 'For the question 'Are acquired characters hereditary?' it would be more accurate to substitute 'Can the acquired characters of the parent be handed down as inherent characters in the offspring?'' (p. 144).

(2) 'It is in no way necessary that the acquired elements of a character should be disentangled from the inherent elements, if only we can prove that the character as a whole is dependent upon a controllable external cause, and is therefore itself controllable. In fact we speak of a character as 'acquired' just as we speak of an article as 'manufactured', although the result itself is a complex

His teachings have led to the general, but not the universal, abandonment of the Lamarckian element in evolution as Darwin conceived of it. They receive support from the numerous Mendelian and Mutationist researches which lead to the conviction that variation is essentially of germinal origin.

Weismann's conceptions of evolution are as much affected by the facts of adaptation as were those of Darwin himself, and he is equally convinced that the onward progress of evolution has been by small steps and not by large ones.

In speaking of 'acquired characters' it may not be out of place to point out that *every character* contains acquired elements, because environmental influence of some kind is necessary for the existence of all characters. When the differences between corresponding characters in different individuals can be traced to *environmental influences* the characters are called *acquired*, when they can be traced to *germinal influence* they are called *inherent*. 'Environmental influence' is here used in the broadest sense and includes the other parts of the same organism. Thus the use or disuse of a part, when determined by the brain, is no less an acquired character than when it is imposed by the conditions of the external world.

of the properties of natural substances and of changes introduced by art' (p. 144).

(3) 'Whenever change in the environment regularly produces appreciable change in an organism, such difference may be called an acquired character' (p. 143).

HUGO DE VRIES considered himself led by his work on the Evening Primroses and by confirming Galton's law of 'recession towards mediocrity', to the conclusion that evolution proceeds by Mutation or Transilience alone, and that individual differences, called by him 'fluctuations', do not lead to marked or permanent change. He does not hesitate to conclude that 'fluctuations' are both hereditary and acquired, and that evolution proceeds by the intermittent explosive discharge of an internal transforming force. According to de Vries, the rôle of Natural Selection is to determine the survival of the fittest among the Mutations scattered in all directions by species during their explosive periods.

GREGOR MENDEL. The thoughts of this wonderful man should follow those of Darwin, but his great discoveries were so long lost to the world, that their final recognition has produced the most recent of all the phases of evolutionary thought. We are led by Mendel's researches, which it is unnecessary to describe, to the conception of 'unit characters':—

'By a unit character in the sense of Mendel's law, we mean any quality or part of an organism, or assemblage of qualities or parts, which can be shown to be transmitted in heredity as a whole and independently of other qualities or parts.'¹

We are also led to the conclusion that a unit character is represented in the germ-cell by a

¹ W. E. Castle, in *Fifty Years of Darwinism* (1909), 146.

determinant (which may consist of one or several factors) or by many linked determinants. For those who hold that the transformation of species proceeds not by the modification but by the addition of new or the subtraction of old unit characters (in the above sense) these conclusions, founded on Mendelian research, are of supreme importance in evolution. Professor Bateson has recently prophesied :—

‘ . . . we see Variation shaping itself as a definite, physiological event, the addition or omission of one or more definite elements; and Reversion as that particular addition or subtraction which brings the total of the elements back to something it had been before in the history of the race.’¹

To those who believe that the outcome of Mendelian research does not bring any essential change in the conception of evolution received from Darwin, the results are still of supreme interest and importance. Just as the splendid cytological work of the past half century helps us to form a picture of the mechanism of fertilization and of heredity but does not alter our conceptions of evolution, so is it with Mendelian research. Upon fertilization and heredity it sheds an even stronger, surer light than that thrown by cytology. We are enabled to understand by the help of examples which obey Mendel’s law something of the general, perhaps the universal, mechanism of heredity. This performance and the promise of deeper knowledge in the future

¹ *The Methods and Scope of Genetics*, Cambridge (1908), 48.

are enough to stamp Mendel's discovery as among the greatest in the history of the biological sciences. But it does not alter the Darwin-Wallace conception of evolution in nature.

The pattern of each mimetic form of the polymorphic female of *Papilio dardanus* is a complex unit character as defined by Castle, yet all of them exhibit clear evidence of a past history of 'continuous' improvement in the likeness to their respective models.

Sports such as those which arise by the dropping out of some definite element and the consequent sudden change to white of the whole or a part of the pigment of an animal or flower, are a type of the appearances which are attractive and interesting to man, and have become subject to artificial selection. And it is with material thus derived that nearly the whole of Mendelian research has been hitherto concerned. Selection may occasionally operate along similar lines in nature, as when an animal migrates into some snow-covered area, but no one who has reflected much upon the struggle for existence can believe that it is the usual method of evolution.

Similarly with regard to the limited advance that is possible when fluctuating variability is artificially selected. Man is able, in a few generations, to double the percentage of sugar produced by the beet. By selecting for this quality alone, he profoundly modifies the relationship of one particular function to the plant as a whole, and

after a time finds that, within the limited period of his endeavour, he can go no further. But Natural Selection does not operate in this way upon single qualities. Every quality of direct or indirect value to the organism and at the same time the inter-relationships of all qualities, are selected simultaneously. Artificial selection does not give us a true picture of the method of nature.

Darwin, as I have said, held that the steps of evolution were built out of small individual differences. He did not doubt that these could be accumulated by selection, but he was prepared to believe that there would be halts. I have always foreseen that the Mutationist would finally 'hedge' by claiming as mutations the minute differences on which Darwin relied.¹ This tendency is very clearly seen in Mr. Punnett's little book² :—

'Doubtless some of the so-called fluctuations are in reality small mutations, whilst others are due to environmental influence' (p. 72).

'A cursory examination of horticultural literature must convince anyone, that it is by selection of mutations, often very small, that the gardener improves his varieties. Evolution takes place through the action of selection on these mutations' (p. 74).

As the Mutationist comes to study the details of adaptation, and as further fossil records preserved under peculiarly favourable conditions are

¹ *Essays on Evolution*, xxxviii, xxxix.

² *Mendelism*.

carefully examined,¹ we may feel confident that the belief in an evolution founded on large mutations will vanish, and we shall then come back to mutations identical in every respect with the small variations which were for Darwin the steps of evolution.

A humorist has suggested that the Homer controversy should be settled by a general agreement that the *Iliad* was written not by Homer but by another man with the same name. Those who have heralded with such a flourish of trumpets the profound changes which they assume to be necessary in the Darwinian conception of evolution, may yet 'save their face' by calling the same thing by another name.

¹ Dr Arthur W. Rowe's researches on the fossils of the white chalk are an admirable example. See the *Quarterly Review* (July, 1909), 19, 20.

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